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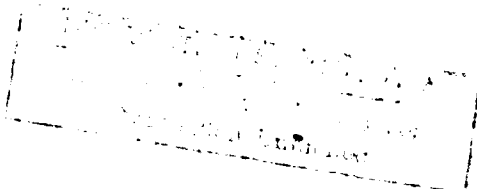
UFFICE OF NAVAL RESEARCH

Grant # N00014-89-J-1582
(Dr Thomas McKenna, Scientific Officer)

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OVERVIEW

The overall goal of this project was to investigate the perception of moving sound sources by the auditory system of barn owl (*Tyto alba*). Although moving sound sources are abundant in the environment, there are surprisingly few studies on acoustic motion perception in species that do not use active echo-location. The barn owl is a keen auditory predator that can capture moving prey in absolute darkness using only passive hearing (Payne, 1971). It therefore served as the model system in which to analyze acoustic motion perception. Using behavior, neurophysiology, and computer-modelling we addressed two large issues:

1) How is velocity, ie, speed and direction, coded in the auditory system?

2) What role does motion play in auditory perception and acoustically-guided behavior?

Our project was thus somewhat of a departure from the traditional study of sound-localization, which generally concentrates on the perception of static sources.

This *Final Technical Report* consists of published (in peer-reviewed journals) and yet unpublished reports that were enabled by our grant from the Office of Naval Research (N00014-89-J-1582, 1989 to 1992). In this "Overview" section, we describe each of these studies briefly. We also include a brief description of a promising, ongoing project that was instigated by our studies of acoustic motion.

Coding of velocity in the auditory system.

Our first studies on motion asked the simple question: Are there cells in the brain of the owl that are sensitive to the direction and/or speed of a

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moving sound source? In collaboration with Dr Herman Wagner[1], we recorded

extracellularly from neurons in the inferior colliculus and optic tectum of

anesthetized owls while broadcasting broadband noise from a semicircular array

of seven loudspeakers. The speakers, located at 30° intervals in front of the

owl, were activated sequentially, thus simulating a source that jumps from

location to location, much as would an owl's prey in nature. The order of

activation, duration, and timing of the noise bursts could be controlled by

computer, thus giving us control over the speed and direction of the simulated

motion (also called "apparent motion"). The inferior colliculus, and despite

its name, the optic tectum, were chosen for study because they contain

auditory neurons that have discrete spatial receptive fields. Like visual-

system neurons they can only be driven if a stimulus is placed at a certain

spatial locus. Furthermore, they are arrayed within these structures

according to the position of their receptive fields so as to form a

topographic map of space.

It was clear, even from our first recordings, that these structures

contained an abundance of neurons that were highly sensitive to the direction

of motion. Typically, a cell would discharge vigorously for motion in one

direction, but weakly if at all for a motion in the opposite direction. Upon

applying a statistical test, we found that the response of over one-third of

neurons in the inferior colliculus and optic tectum were dependent upon the

direction of motion. This dependency on direction stemmed from the fact that

the cells were inhibited by motion simulated in the non-preferred direction.

Probing further, we found that although the neurons seemed to be sensitive to

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direction, they were not sensitive to speed. Their ability to signal the direction of motion remained constant over a wide range of biologically-relevant angular speeds. Furthermore, we discovered that by inserting silent intervals between sounds from successive speakers, the cell's ability to discriminate the direction of movement was diminished. This finding tempts us to speculate that for the owl, there can be a maximum silent interval between samples, below which the target is classified as a single source moving from one location to another, rather than a new stationary sound that has popped up in a new location.

The ability of the cells to discriminate direction, the vulnerability of this characteristic to silent intervals, and the broad tuning for speed were used as constraints to formulate an explicit computational model. This effort was undertaken as a thesis project by Mr Dirk Kautz, a graduate student in the Institute of Neuroscience and the Department of Physics, here at the University of Oregon. Adapting a motion detector formulated for the visual system to the owl's inferior colliculus, Mr Kautz succeeded simulating neurons that can signal the direction in which a stimulus crossed its receptive field. Furthermore, the model predicted that the convergence of information from multiple frequency channels and the lateral interactions between space-tuned neurons were important in enhancing directional sensitivity. These points can now be tested by comparing directional sensitivity obtained with broad-spectrum and narrow spectrum sounds and by interfering with lateral inhibition pharmacologically[2].

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[2] Lateral inhibition can be diminished by the application of bicuciline methiodide, a $GABA_a$-antagonist. (Fujita I, Konishi M, 1991 *J. Neurosci.* 11:722-739.)

The following reports resulted from this aspect of the project and are included in this Final Technical Report.

Takahashi T, Wagner H 1990 Directional sensitivity of auditory neurons in the owl. *Abst. Soc. Neurosci.*

Wagner H, Takahashi T 1990 Neurons in the midbrain of the barn owl are sensitive to the direction of apparent acoustic motion. *Naturwissenschaften* 77:439-442

Kautz D 1992 A computer model for acoustic motion-direction sensitivity in the barn owl. Master's Dissertation, Institute of Neuroscience and Dept of Physics, University of Oregon, Eugene, OR.

Wagner H, Takahashi T The influence of temporal cues on acoustic motion-direction sensitivity of auditory neurons in the owl. In review *J. Neurophysiol.*

The role of motion in auditory perception and behavior.

Given the ubiquity of motion in the natural environment, is the auditory system able to exploit motion to its advantage? There are numerous instances in the visual system showing that motion aids in the perception of stimuli (e.g., Regan et al. *J. Neurosci.* 12:2198-2210). This portion of the project was carried out with Dr Clifford H Keller, a post-doctoral fellow supported, in part by this grant.

Our first study on the influences of motion on acoustic perception demonstrated that a moving acoustic source can be detected in a noisy background more easilty than a stationary source. We demonstrated this by

recording from neurons in the inferior colliculus that are selective for interaural phase difference of a tone, the binaural cue for stimulus azimuth. A cell's ability to detect a tone was assesed by measuring its tuning curve for interaural phase difference under various levels of masking noise. If a phase sensitive cell is unable to detect a tone, its response, plotted as a function of interaural phase difference should be flat, or more specifically, no different from random. This assessment was made under conditions that simulated stationary and moving sources. Stationary tones were simulated by broadcasting tones of identical frequencies to the two ears and changing the interaural phase difference in steps. To simulate motion, we used a stimulus known as "binaural beats". In binaural beats, the left and right ears receive slightly different frequencies, and therefore, the interaural phase difference changes continuosly over time. As interaural phase difference is the binaural cue for sound-source azimuth, the stimulus simulates a tone-emitting target moving at a constant angular speed. We found that when a stationary tone was presented to the ears in the presence of binaurally-uncorrelated masking noise[3] a cell's tuning for interaural phase difference showed a marked decline, suggesting that the cell was less able to detect and signal the presence of the tone. However, if the tone was now moved, using binaural beats, the cell's tuning to interaural phase difference re-emerged. We concluded that the circuitry in the owl's inferior colliculus is capable of exploiting motion in order to break camouflage - a finding similar to the well-known visual effect in which patterns that are undetectable when

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[3] The noise to the two ears come from two independent noise generators. The output of one noise generator is statistically random with respect to that of the other.

stationary become visible when moved. The computational model developed by Kautz (above) is currently being used to generate possible interneuronal connections in the inferior colliculus that may account for this phenomenon.

In the original proposal, we hypothesized that motion may be useful in determining the distance to a sound source. Although the work is still ongoing, we have succeeded in showing that a barn owl will focus its eyes on a sound source. A barn owl is trained to stand quietly on a perch in a dark room while sounds are broadcast to it through a row of loudspeakers, or through a small, motorized, radio-controlled target. The accomodative state of its eyes are monitored by a infrared photoretinoscope (Schaefel et al. *Applied Optics* 26:1505-1509) mounted on a video camera. Our results thus far show that when a target, whether real or simulated, approaches the owl, its eyes focus near and when the target recedes away from the bird, its eyes focus far. We are unable to conclude whether owls are able to detect the distance to a stationary target that emits but one burst of sound. At least one trained bird is able to perform this task, but we are uncertain of the cues it is using.

We plan to continue studying the issue of motion and distance coding behaviorally, by altering various sound parameters such as overall loudness or spectral profile, and neurophysiologically by recording from neurons in the inferior colliculus while broadcasting sounds from different distances or by simulating motion along the range-axis.

The following reports were generated in this phase of the project and are included in this Final Technical Report.
Takahashi TT, Keller CH Motion unmasking of auditory targets. Invited paper

to be presented at the *Third Int'l Congress of Neuroethology* August 9–
14, 1992.

Takahashi TT, Keller CH Enhancement of neuronal selectivity to a sound
localization cue by simulated motion in background noise. *J. Neurosci.*
in press.

Keller CH, Takahashi TT Discrimination of target distance from sound alone by
the barn owl (*Tyto alba*). Technical report to ONR.

The imaging of multiple acoustic sources: An ongoing project.

The owl's inferior colliculus contains a generalized circuitry that
converts interaural cues into foci of neural activity on a topographical map.
Our motion studies suggested that these foci are more discrete for moving
stimuli. Since the environment contains many concurrent sound sources it is
natural to ask how this generalized circuitry would image multiple,
concurrently-active sound sources? While this problem is trivial in neural
maps of visual or somatosensory space, it becomes particularly interesting in
the imaging of acoustic targets. Sounds from multiple sources will sum
vectorially at the eardrums, and therefore, if two concurrently active sources
broadcast similar spectral components, the binaural cues that result for these
frequencies will indicate a phantom image at an erroneous location. We
hypothesized that if the spectra from the sources contain components that are
unique to each source, the brain may have a basis from which to parse the
complex waveforms at the ears into neural images on appropriate locations in
the map.

Two computer modellers, Mr Michael Fleming and Mr Will Goodwin[4], and I first tested the feasibility of this idea by simulating the owl's inferior colliculus on computer (SPARC Station 2, Sun Microsystems) using a method called "back propagation". We endowed an input layer of simulated neurons with the selectivities for frequency and interaural phase difference found in neurons of the central nucleus of the inferior colliculus. A different computer program randomly generated multiple "sources", each at a different spatial location and broadcasting sounds with randomly-chosen spectra. The program coverted the sounds into the composite phase and amplitude spectra that would be expected at the ears and activated the appropriate neurons in the input layer. The input layer was connected to simulated neurons in an output layer each of which represented a point in space. The connectional weights between cells in the input and output layers were adjusted by training with a standard back propagation algorithm. The network could be trained in about 1000 trials, and when trained, it could parse multiple sources provided that the sources broadcast spectra that were different.

An examination of the connectional weights revealed that the neural network arrived at a solution that was extremely similar to the anatomical connection that operates in the owl's inferior colliculus. This suggested that the problem of multiple targets can be solved by a network that has the properties found in the owl's auditory system.

Our present efforts are aimed toward mapping the neural image formed in the owl's inferior colliculus by multiple targets and determining the acoustic

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[4] Mr Michael K Fleming is currently enrolled in the graduate program in the Department of Psychology, Stanford University. Mr William J Goodwing took over the project when Mr Fleming left to attend graduate school. Their vitae are enclosed.

conditions that influence the resolving power of this neural map of space. In addition we are continuing to develop the computer-simulated "inferior colliculus", by making it capable of accepting sounds from a spectrum analyzer equipped with two microphones. The network, with its similarity to its biological counterpart, can then be used to generate further physiological tests. Moreover, we see many potential uses for the computer neural network itself as a general acoustic imaging device.

The following report was generated from this aspect of the project and is included in this Final Technical Report:

Fleming MK, Goodwin WJ, Takahashi TT 1992 Topographic representation of multiple acoustic targets by a neural network. *Abst. Soc. Neurosci.* (To be presented at the 1992 Annual meeting of the Society for Neuroscience)

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DIRECTIONAL SENSITIVITY OF AUDITORY NEURONS IN THE OWL.
T.T. Takahashi and H. Wagner. Institute of Neuroscience, University of Oregon, Eugene, OR 97403; Max-Planck Institut für Biologische Kybernetik, D-7400 Tübingen, FRG.

The barn owl captures moving prey using only its sense of hearing. To study the neural basis of sensitivity to moving sound sources, we recorded the responses of 68 neurons in the owl's superior and inferior colliculi to the motion of a target simulated by sequentially activating 7 speakers placed at 30° intervals in the horizonal plane. Stimuli were typically 100-msec bursts of broadband noise, presented every 95 msec, simulating a speed of 102°/sec. The response of the neurons were plotted as post-stimulus time histograms to determine whether spike discharge was greater in one direction than in the other. As a control, we disconnected all speakers except the most effective speaker and repeated our stimulus presentation. The single speaker condition, which contains no motion cues, represents a reference with which to judge the directional preference of a neuron statistically (chi-squared). Of the total, 37% displayed a significant directional preference. Inhibition in the null direction (89% of cells) facilitation in the preferred direction (11%), and both (11%) accounted for directional sensitivity.
(Supported by grants from the Office of Naval Research (N0001489J1582) and the Deutsche forschungs Gemeinschaft [SFB 307].)

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KEY WORDS: (see instructions pg. 4)

1. Motion
2. Acoustic
3. Optic Tectum
4. Inferior Colliculus

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Neurons in the Midbrain of the Barn Owl Are Sensitive to the Direction of Apparent Acoustic Motion

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An animal's environment is rarely static. Stimuli from moving sources abound, and, in one sensory system, vision, the neurological basis of motion processing has been well characterized on experimental [1 – 3] and theoretical grounds (for a recent review see [4]). The acoustic environment is no less dynamic. Psychophysical studies have shown that while we are less sensitive to the movement of a sound source than that of a visual stimulus, our ability to judge direction and speed, once we detect the motion, is as accurate as that for vision [5 – 7]. Nevertheless, the neural basis of acoustic motion perception has not received the attention that has been devoted to visual motion processing or the localization of stationary sound sources. The barn owl (*Tyto alba*), whose ability to localize sound has been extensively studied [8, 9], is also known to be able to judge the direction in which prey are moving [10].

We report here the existence of mesencephalic neurons whose response depends upon the direction of apparent acoustic motion, in short, are motion-direction sensitive.

Recordings were made in three adult barn owls. Anesthesia, surgery, perfusion, histological localization of lesions, and animal care were described earlier [11]. All recordings were made in an anechoic chamber ($3 \times 3 \times 3$ m). Search stimuli consisted of tone or noise bursts having an interaural time difference and interaural level difference, important cues for azimuthal and elevational sound localization in the barn owl, respectively [8, 9]. The search stimuli were presented dichotically over stereo earphones (Sony MDR-E272). After a cell was identified we switched from dichotic stimulation to stimulation through seven 10-cm speakers arranged in a semicircular array about $10°$ below the owl's horizon (inset, Fig. 1). Speakers were placed at $30°$ intervals from $+90°$ (owl's right, speaker #1) to $-90°$ (owl's left, speaker #7).

[11, 13 – 15]. All neurons that responded to stationary stimuli responded also to the apparent motion stimulus. In about 70 % of the recordings, maximal spike rate in the stationary condition equaled the maximal spike rate in the motion condition. In 15 %, the response was better to motion, and in 15 % the response was better to stationary stimuli.

The PST histograms in Fig. 1 demonstrate a neuron with high motion-direction sensitivity. The speaker array was first activated in the counterclockwise direction (ccw), from speaker #1 to #7, then, in the clockwise direction (cw), from #7 to #1 (Fig. 1a). A strong discharge could be associated with the activation of speaker #3 when the array was activated in the counterclockwise direction, but not when the array was activated in the clockwise direction. This resulted in a PST histogram with a DI of 0.82 (Fig. 1a). To exclude the possibility that this was simply an onset effect, we reversed the activation sequence, beginning with clockwise motion followed by counterclockwise motion (Fig. 1b). Under these circumstances as well, the neuron discharged heavily during counterclockwise motion, confirming that it was direction and not stimulus onset that was responsible for the asymmetry of the PST histogram (DI = 0.77). When only the most effective speaker, #3, was enabled, the neuron responded twice per roundtrip or each time speaker #3 emitted a sound. This resulted in a symmetrical PST histogram and a low DI of 0.07 (Fig. 1c). The PST histogram of Fig. 1c further demonstrates that the single burst, caused by the first activation of speaker #3, did not fatigue the neuron. Finally, comparison of the top two histograms with the bottom histogram revealed that the number of spikes in the nonpreferred, or "null", direction was less than that evoked by the activation of speaker #3 alone, and that the maximum number of spikes per bin in the preferred direction was similar to the number of spikes in the stationary test. Therefore, this neuron's motion-direction sensitivity was due to an inhibition in the null direction.

The distribution of all DI values is shown in Fig. 2. Of the total number of 68 cells, some 34 % had a statistically significant DI. These DI values are
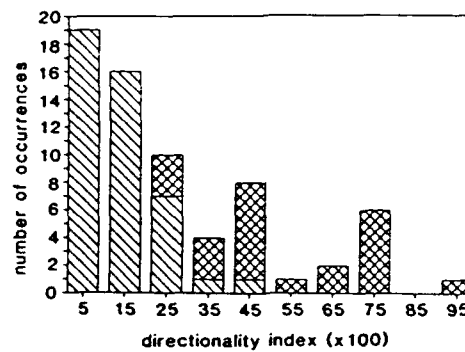

Fig. 2. Distribution of directionality indices. Of the 68 recordings, the directionality indices of the motion-direction insensitive cases are plotted by the *lightly hatched bars*, those of the motion-direction sensitive cases (chi-square test, $p < 0.05$) by the *cross-hatched bars*. Stimulus conditions for all recordings were as noted in Fig. 1. If more than one test was performed with a cell, all spikes registered in response to clockwise and all to counterclockwise stimulation were summed for the calculation of the DI value and the chi-square test. Some cells, like that shown in Fig. 1, showed onset responses. Such responses were excluded from the analysis. Bin width is 0.1
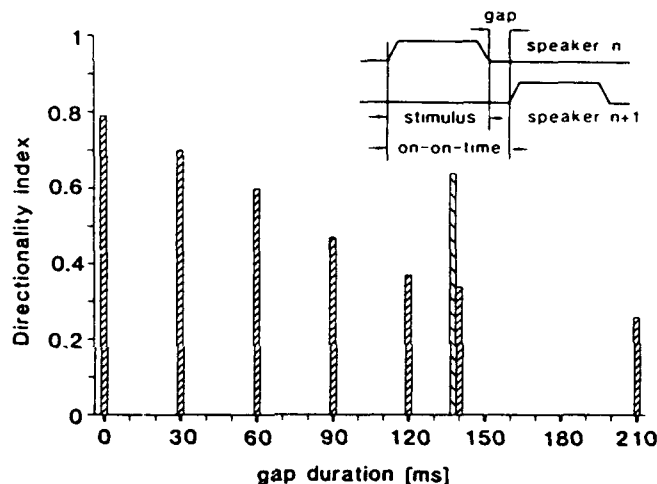

Fig. 3. Dependence of the DI value on gap duration. In the *inset* the relation between on-on time, stimulus duration and gap duration is shown. As the on-on time of 240 ms, equivalent to an apparent velocity of 125°/s, was kept constant, the DI value decreased with increasing gap duration in this neuron (*heavily hatched bars*). The *lightly hatched bar* shows the DI value for an on-on time of 95 ms and a stimulus duration of 100 ms, a parameter combination that reduced the gap to zero. Note that this bar is plotted next to the bar with the same stimulus duration but 140 ms gap duration under the 240 ms on-on time condition

scattered in the upper half of the distribution and are responsible for its long tail. To judge whether motion-direction sensitivity was due to an inhibition in the null direction, wherein the response in the null direction is less than the stationary response, or to a facilitation in the preferred direction, wherein the response in the preferred direction is greater than the stationary response, we compared the responses in the motion condition with that in the stationary condition. Inhibition in the

null direction was observed in 89 % of the cases. Facilitation in the preferred direction occurred in 22 % of the neurons, and 11 % of the neurons showed both inhibition in the null direction and facilitation in the preferred direction.

Further evidence for inhibition as a major factor in generating motion-direction sensitivity under our stimulus conditions came from experiments in which a gap was introduced between the activation of a speaker and the activation of the next speaker. To in-
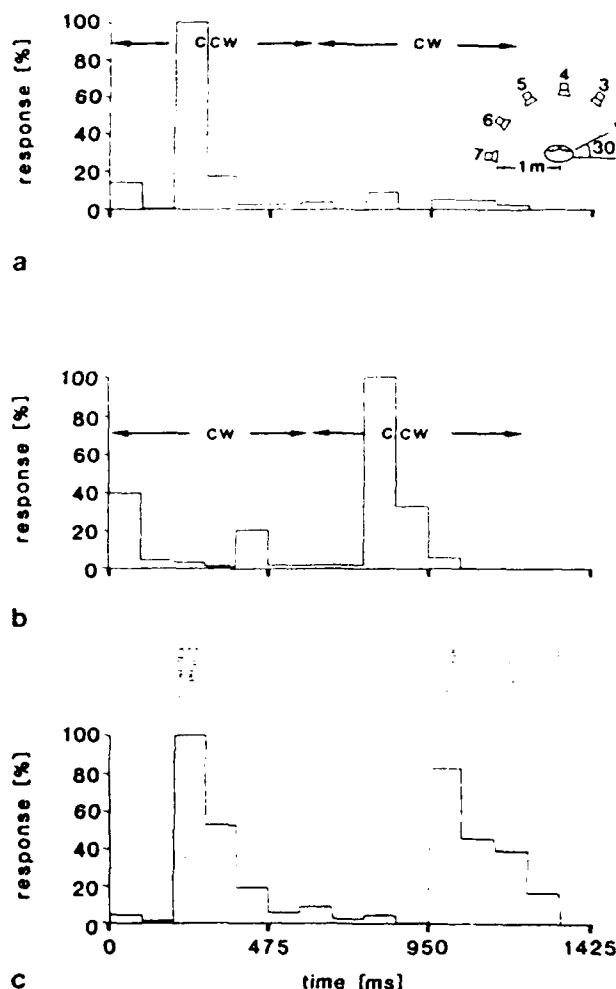
Fig. 1. Tectal cell sensitive to the direction of apparent acoustic motion. The cell responded much better to counterclockwise motion (ccw) than to clockwise motion (cw) irrespective of whether the motion started in the counterclockwise direction (a) or the clockwise direction (b). A dot-raster display demonstrating the spike discharge to 20 roundtrips is shown above each PST histogram. The maximum of the response was 130 spikes in (a) and 88 in (b). If only the most effective speaker in the motion conditions (a, b) was enabled on (c), a symmetrical PST histogram resulted, but the response maximum was still high (112 spikes). The onset response of this neuron, occurring in the first 100 ms after the beginning of the roundtrip (a, b), was excluded from the analysis. The DI values in the motion conditions are statistically significant at the $p < 0.01$ level. On-on time was 95 ms, and successive stimuli overlapped in time by 5 ms or the rise/fall time of the individual bursts. The units of analysis (bins) in the PST histograms correspond to the on-on time. In the *inset* the loudspeaker arrangement is shown

Speakers were sequentially activated in a "roundtrip" pattern, which simulated a source moving from 90° on one side to 90° on the other side, and back. Successive roundtrips were separated by 3 to 7 s of silence. Stimuli from the individual speakers consisted of noise bursts (flat between 1 and 25 kHz) having 5 ms rise/fall times and variable durations. For most of the experiments, the earphones were left in place, because control experiments revealed that a neuron's motion-direction sensitivity was unaffected by the presence of the earphones. The duration of the stimulus, the interval between the onset of successive sounds ("on-on time"), which determines the velocity of the apparent motion, and the overlap or silent interval ("gap") between successive sounds (inset, Fig. 3) were controlled by a computer (IBM AT). Note that only two of these three variables can be chosen independently.

The time of arrival of action potentials, relative to the onset of the roundtrip, was recorded in computer memory and analyzed as peristimulus time (PST) histograms. To quantify the motion-direction sensitivity of a neuron, we derived a directionality index DI:

DI = 1 − (lower spike count/higher spike count).

"Lower spike count" and "higher spike count" refer to the halves of the PST histogram with the lower and higher numbers of spikes, respectively (Fig. 1). To judge the statistical significance of the DI, we compared, using a chi-square test, the halves of the PST histogram from trials in which all speakers were enabled (motion condition), with those from trials in which only the most effective speaker produced a sound (stationary condition). The stationary condition represents the null hypothesis for the chi-square test, because a symmetrical PST histogram is expected if only the best speaker is activated twice each roundtrip. When a cell was lost before the stationary test was performed, the spike counts to clockwise and counterclockwise stimulation were averaged for the chi-square test. This was always done to test for a bias in the one-speaker test. One cell out of 50 tested with the stationary condition was biased and was excluded from the further analysis.

The results are based on 68 recordings from the optic tectum (17 recordings), the external nucleus of the inferior colliculus (ICx) (9), and the lateral shell of the central inferior collicular nucleus (ICc-ls) (30). The remainder of the recordings (12) lay also in the vicinity of these nuclei, but the association of a recording with a specific nucleus was not possible in these cases. Anatomical studies have shown that ICc-ls projects to the ICx, which, in turn, innervates the optic tectum [11, 12]. About two-thirds of the recordings were isolated as single units. No difference in the response to moving stimuli was seen between single-unit recordings and multi-unit recordings. The general response characteristics of these neurons to stationary sound bursts are well known

troduce the gap, apparent velocity was kept constant while stimulus duration was decreased. As the gap increased, motion-direction sensitivity decreased (Fig. 3). In contrast, the response level was independent of gap duration (not shown). The smooth decrease of DI with gap duration seen in Fig. 3 could not be explained by a decrease in the sound energy that resulted from the decrease of stimulus duration, because for a stimulus duration of 100 ms, a much higher DI value resulted for a zero gap than for a gap of 140 ms (Fig. 3, lightly hatched bar). Seventeen of the 23 motion-direction sensitive cells were stimulated with more than one combination of on-on time and gap duration. For zero gap duration and upon variation of the apparent velocity, the DI varied only slightly. The mean DI changed from 0.50 for 125°/s ($N = 11$) and 0.53 for 310°/s ($N = 23$) to 0.41 for 1000°/s ($N = 10$). If, however, in the case of 125°/s a gap was introduced so as to generate the same stimulus duration as in the 1000°/s case, the mean DI was only 0.25 ($N = 11$).

Our results demonstrate that a large proportion of neurons in the midbrain of the barn owl is sensitive to the direction of apparent acoustic motion in the horizontal plane. Our sample may underestimate the actual number of motion-direction sensitive neurons because we only assessed motion along the horizontal axis, and, because our dichotic search stimulus simulated a stationary source.

Earlier neurophysiological studies of mammals have also demonstrated motion-direction sensitivity in auditory neurons by a variety of techniques [16 – 19]. The earlier studies relied on the inspection of neuronal spike trains and PST histograms rather than on a statistical analysis to judge the motion-direction sensitivities. In these studies motion-direction sensitive neurons were not as common as in the owl's midbrain, independent of stimuli used, e.g., dichotic clicks [16], binaural beats [17] or apparent motion [18].

Although most of our motion-direction sensitive cells were found in the optic tectum, it is of interest to note that some of the cells in the ICc-ls were motion-direction sensitive. Unlike the optic tectum or the ICx, the ICc-ls is composed of cells that are sharply tuned in frequency and have multiple spatial receptive fields [11, 13]. Cells in the tectum and ICx have a single spatial receptive field, which is a consequence of having a broad frequency selectivity [11, 13 – 15]. Not only does this suggest that motion-direction sensitivity can precede the formation of space-specific cells that have unique spatial receptive fields, it also implies that the motion-direction sensitive cells have the ability to preserve the spectrum of the moving sound. Such capability, we speculate, may signal to higher centers that a particular group of frequencies moved in unison, and can therefore be treated as having a common origin.

Many neurons responded to stationary as well as to moving stimuli. Therefore, these neurons cannot signal whether or not a source is moving without further neural computation. We have shown that inhibition is a major factor in generating the acoustic motion-direction sensitivity in the barn owl. In some 22 % of the cells facilitation in the preferred direction was also found. These data are in accord with models of motion detectors that require a nonlinear, notably inhibitory interaction between two inputs as proposed for visual motion detectors [1]. They do not, however, exclude the possibility of excitatory interactions in detection of acoustic motion. More experiments, with various sound levels, different acoustic characteristics (e.g., tones, clicks), and various spatial arrangements of the sound sources are necessary to analyze the mechanisms underlying the detection of acoustic motion and to determine whether they closely resemble visual motion detection mechanisms [1 – 4] in their implementation, or, whether acoustic-motion detection mechanisms are different.

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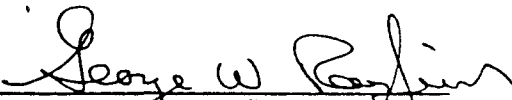# A COMPUTER MODEL FOR ACOUSTIC MOTION-DIRECTION SENSITIVITY

IN THE BARN OWL

by

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A THESIS

Presented to the Department of Physics
and the Graduate School of the University of Oregon
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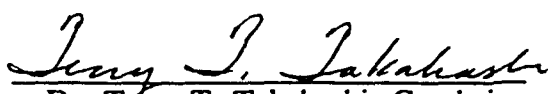
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Computational models that include as much experimental data as possible enable the neuroscientist to better understand complex, nonlinear brain systems. Here, aspects of the auditory system of the barn owl that are concerned with the perception of moving sound-sources are analyzed using a general-purpose simulator for biological neural networks. Recent experiments have demonstrated neurons in the owl's midbrain that are sensitive to the direction of motion.

The model was constrained by anatomical and physiological data although some additional assumptions were made. The model consists of three layers, each of which corresponds to a nucleus in the owl's midbrain. The layers are composed of simulated neurons exhibiting responses similar to real neurons.

It was found that convergence as well as lateral inhibition improved the directional response of output layer neurons. Phase shifting the frequency channels against each other only lead to a slightly lowered directional response.

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ACKNOWLEDGMENTS

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CHAPTER I

INTRODUCTION

Computational models that include as much experimental data as possible enable the neuroscientist to better understand complex, nonlinear brain systems (Sejnowski et al., 1988). Here, a computational model using the general-purpose simulator for biological neural networks, GENESIS (Wilson et al., 1989), is described which served as an aid in the analysis of responses of acoustic motion-direction sensitive neurons in the owl's midbrain (Wagner and Takahashi, 1990; Wagner and Takahashi, in press; Takahashi and Keller, in press).

This introduction presents what is known about the neural substrates underlying stationary sound localization by the barn owl (Tyto alba, hereafter referred to as the owl). Experimental and theoretical studies on visual and acoustic motion detection are reviewed briefly. The distinctive features of the auditory system of the barn owl are discussed and suggestions are made on how to integrate concepts developed for modeling of the visual system into this framework.

Space-Specific Neurons in the Midbrain of the Barn Owl

An important, but challenging task for the auditory system is the localization of sound sources. Whereas in the visual system, locations of objects are projected onto the retina, thereby providing a natural topology, the auditory system must rely mostly on
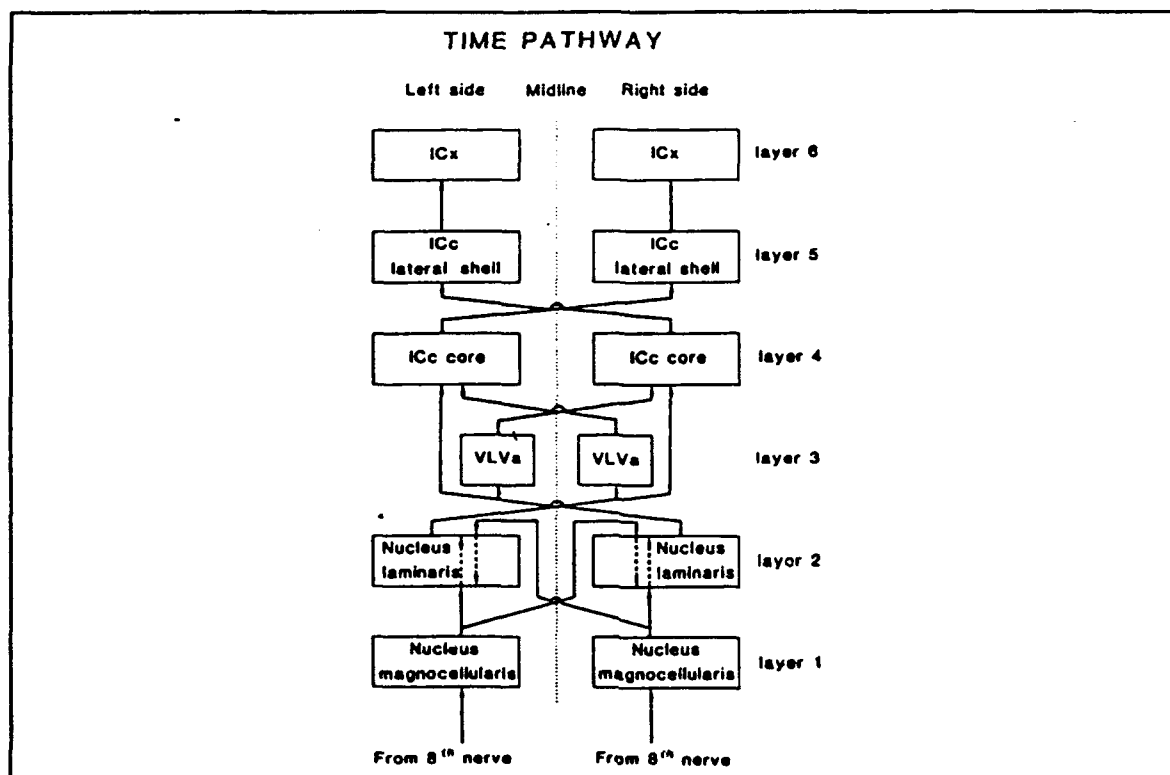
Fig. 1. The time pathway of the auditory system of the barn owl. [Taken from Wagner (1990)]

binaural disparities for sound localization (for a general review, see Blauert, 1983; for a review of the psychophysical literature on sound localization, see Middlebrooks and Green, 1991; for a review of the owl's auditory system, see Takahashi, 1989).

At the beginning of the neural pathway, amplitude, phase, and frequency of sound are carried by the auditory nerve (8th nerve, see Fig. 1). Due to its unusual, asymmetrical head shape the owl is able to use interaural time (ITD) and intensity differences (IID) to signify the azimuth and elevation of a sound source, respectively (Knudsen and Konishi, 1978c; Moiseff and Konishi, 1981; Moiseff, 1989a,b). The auditory nerve terminates in the two cochlear nuclei, and from there on, the owl's auditory system processes ITD and IID in anatomically and physiologically separate pathways (Konishi, 1986; Konishi et al., 1988). In both pathways the signals are

processed initially in several distinct frequency channels deriving from the tonotopical organization of the cochlea.
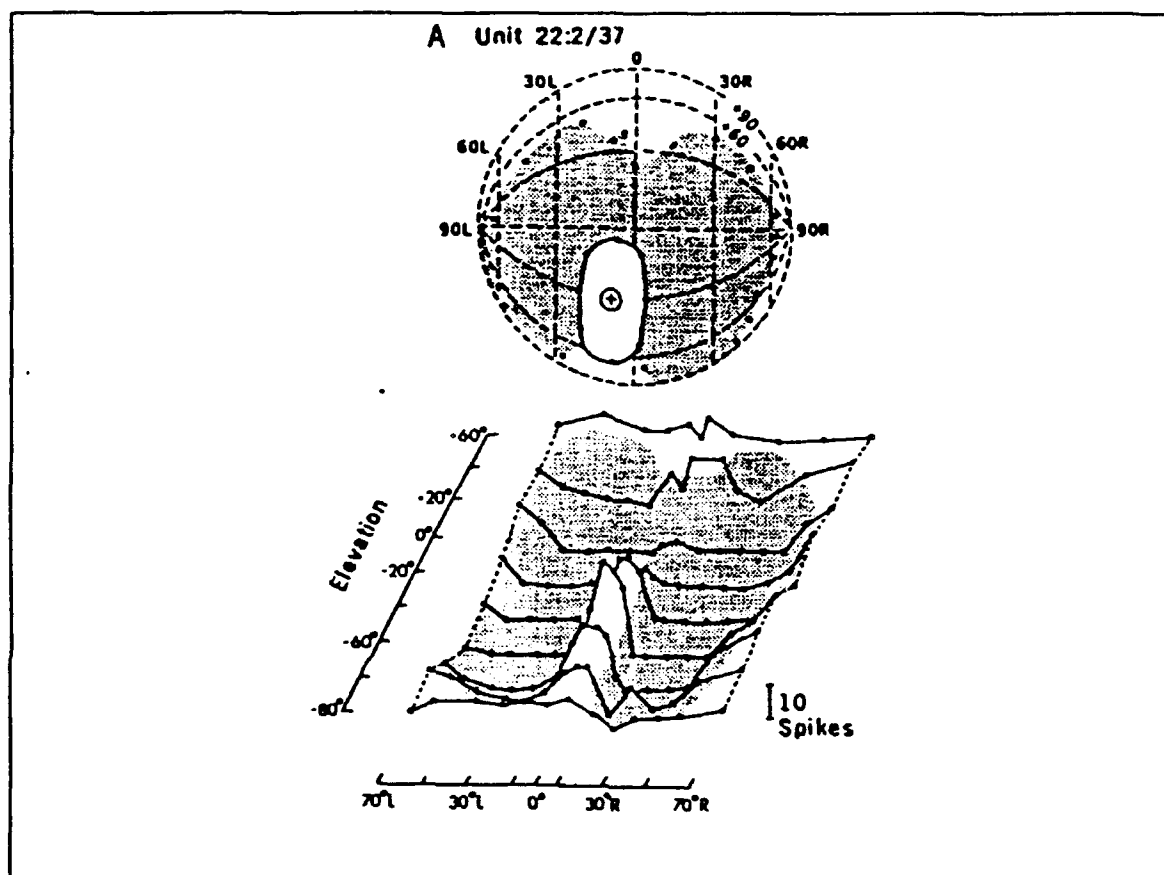
Fig. 2. The center-surround receptive field of a "space-specific" neuron. Inhibitory areas are stippled. The model only deals with the x-axis (azimuth of the sound source) of the figure displayed in the lower half. [Taken from Knudsen and Konishi (1978c)]

Information from both pathways and different frequency channels is finally integrated in the neurons of the external nucleus of the inferior colliculus (ICx). There, a so-called "space map" exists wherein neurons are activated best if a sound source is placed at a well defined location in space (the spatial receptive field of that neuron, see Fig. 2). As in the visual cortex, these "space-specific neurons" are organized in a map-like fashion, preserving neighbor relationships of points in space (Knudsen and Konishi,

1978a; Knudsen et al., 1987). Note that this map of auditory space has to be computed from binaural cues - it is not the result of the simple preservation of the receptor epithelium's surface topography.

This thesis concentrates on the upper three layers of the schematic diagram shown in Fig. 1: the core of the inferior colliculus (ICc core), the lateral shell of the inferior colliculus (ICc-ls) and the external nucleus of the inferior colliculus. All three are cell-groups or "nuclei"[1] in the midbrain. Parts of the midbrain are also involved in the control of eye movements. The periphery of the auditory system (Fig. 1) will not be modeled here, however, it might be interesting to provide this model with input from realistic models of the auditory periphery (Sullivan, 1990; see also Deng, 1992) in future studies.

Phase Ambiguity in the "Time Pathway"

Since more is known about the computation and representation of interaural time difference, the proposed computer model shall deal exclusively with the horizontal coordinate of sound sources which is computed by the "time pathway" (Fig. 1).

The difference in arrival time between the first wavefronts of the sound at the near and far ears, called the onset-time disparity, is related to the azimuthal coordinate of the sound source (Fig. 3; Blauert, 1983).

However, the critical parameter in ITD sensitivity of neurons in the central nucleus of the inferior colliculus (ICc) - which send their output directly to the space-specific neurons mentioned above - is not onset-time disparity (Δt), but interaural phase difference ($\Delta \Phi$) (if one assumes a periodic signal).

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[1] A discrete cellular group, distinguishable from others on electrophysiological, anatomical and biochemical grounds is called "nucleus" (e.g. Kandel et al., 1991)
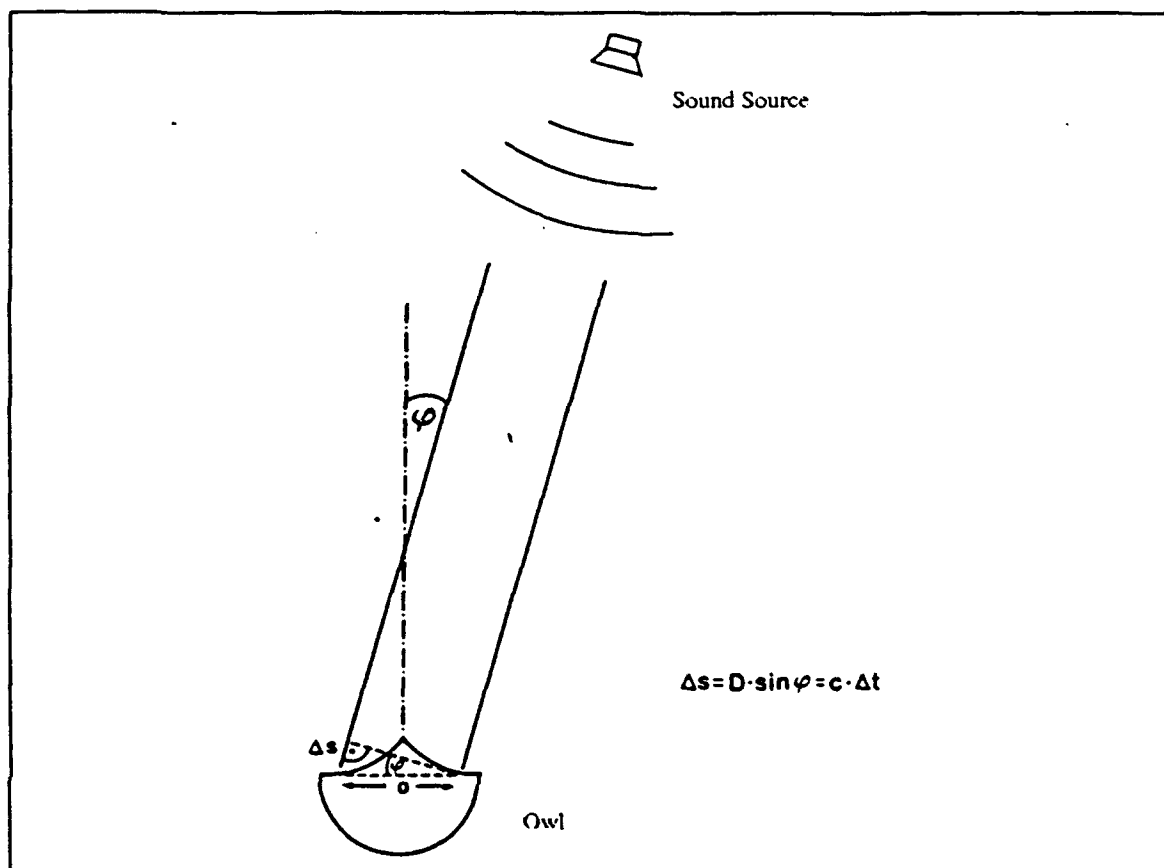
Fig. 3. The difference in arrival time of the sound wave in the two ears ($\Delta t = \Delta s/c$ where c is the speed of sound) is related to the azimuthal coordinate (φ) of the sound source. (D = distance between the ears). [Taken from Grün (1991)]

Neurons in ICc are tuned to a narrow band of frequencies and tonotopically organized (Wagner et al., 1987). Since for a given frequency not only Δt, but also all interaural time disparities, $\Delta t + z \cdot \tau$, where $\tau = 1/BF$ is the period of the best frequency (BF) of the neuron and $z \in I$, yield the same phase disparity $\Delta \Phi$, interaural time differences and hence horizontal locations are represented ambiguously by one phase-tuned neuron alone. However, because of the linear relationship between phase difference and frequency f,

$$\Delta \Phi = 2 \pi \Delta t \cdot f \qquad (1)$$

a group of neurons tuned to different frequency bands can be used to signal a unique interaural time difference.
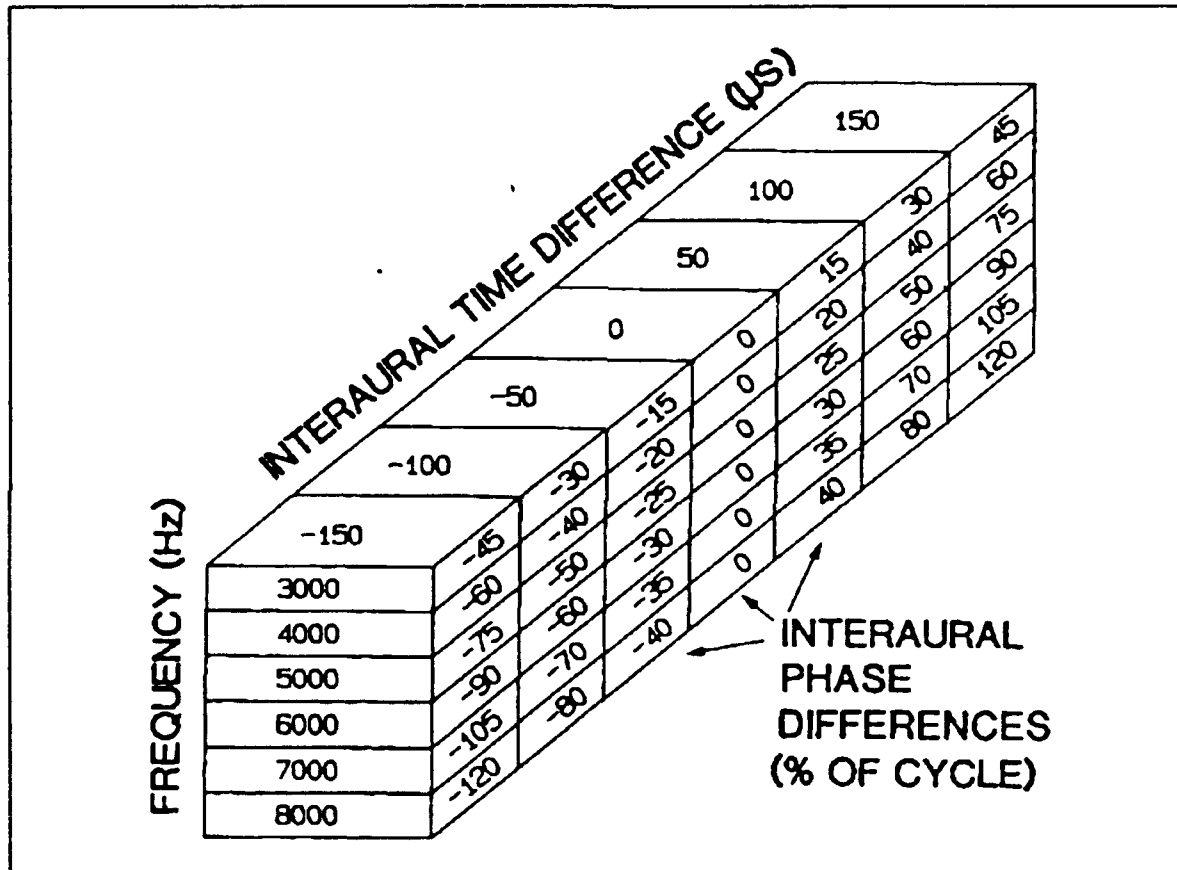
Fig. 4. Schematic model of the ITD-sensitive region of the central nucleus (ICc). The frequency laminae are represented from top to bottom; auditory space is represented by the array-specific ITD's from left to right. [Taken from Wagner et al. (1987)]

Wagner et al. (1987) showed that indeed, neurons in the ICc are organized in arrays (or columns), each array containing neurons whose preference to $\Delta\Phi$ and frequency, respectively, fit Equation (1). Their model is shown in Fig. 4. It should be noted that neither this model nor the computer model presented here with its discrete frequency channels represent the biological reality accurately, where parameters are mapped in a
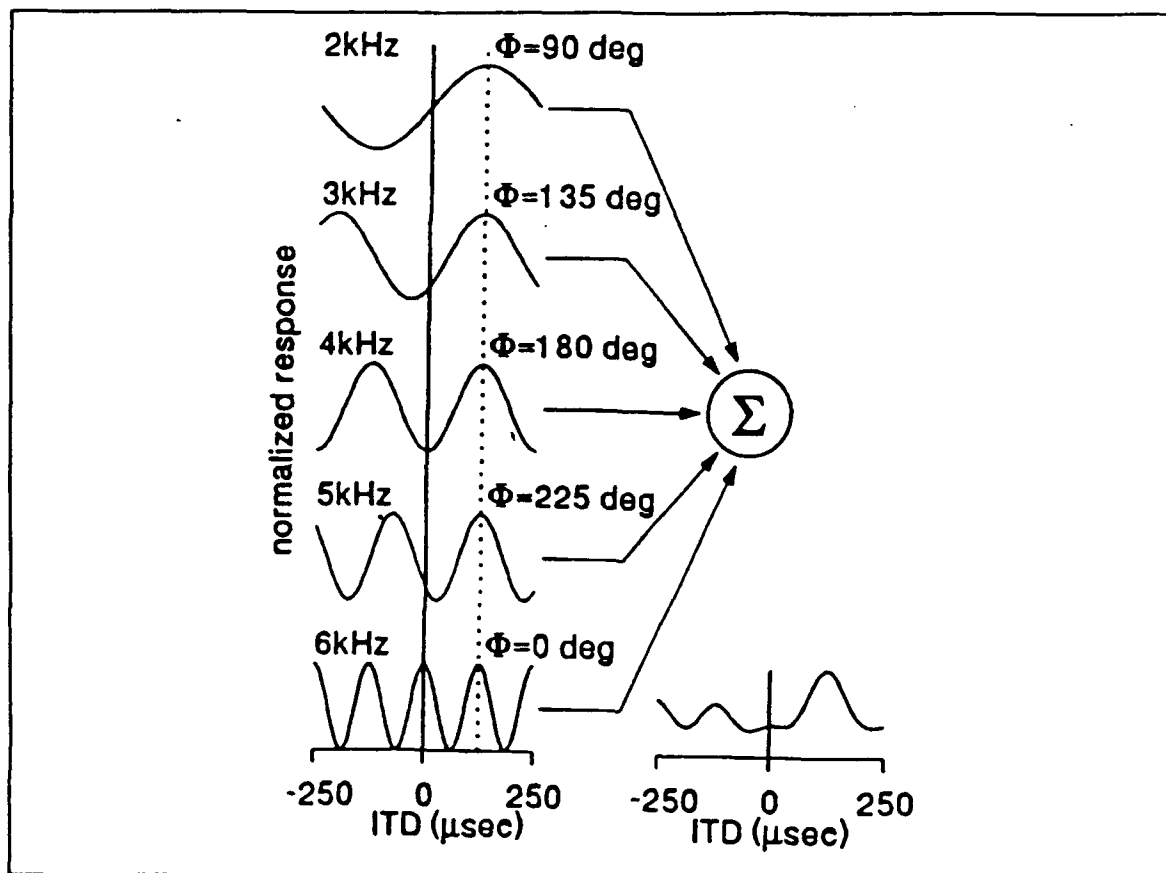
Fig. 5. The projection of neurons in the ICc-ls tuned to different frequencies onto one ICx neuron unambiguously signaling ITD. [Courtesy of H. Wagner]

continuous fashion. The space map neurons in the ICx combine input from many frequency channels in a yet unknown, nonlinear way to code unambiguously for interaural time difference (Fig. 5; Takahashi and Konishi, 1986; Brainard et al., 1992). Note that the neurons in the ICx consequently respond to a much broader band of frequencies (between 3 and 9 kHz) than neurons in the ICc do.

Acoustic Motion Detection

The specific neural computation to be modeled here is the response of a subset of neurons in the time pathway to moving sound sources. Wagner and Takahashi (1990 and

in press) and Takahashi and Keller (in press) found motion-directionally sensitive neurons in various midbrain nuclei of the owl, including the ICc and the ICx. Motion-directional sensitivity indicates that the neurons responded better to a sound source moving in one azimuthal direction (preferred direction) than in the opposite direction (null direction). Wagner and Takahashi (in press), using an apparent motion paradigm, found some 30% of the neurons sampled in all subdivisions of the inferior colliculus and the optic tectum to be motion-direction sensitive. Takahashi and Keller (in press), presenting tones that simulated moving sound sources dichotically, found little directional preference in neurons sampled from ICc. They reported a sharper tuning of cells in the ICc for $\Delta\Phi$ in response to simulated moving as opposed to simulated stationary sources. The experiments by Wagner and Takahashi (in press) suggest that a mechanism which suppresses the response in null-direction plays an important role.

In the visual system, there is good evidence for neural systems specialized for the detection of motion (for a recent review, see Borst and Egelhaaf, 1989). It is now widely accepted that motion is initially evaluated in parallel by an array of "local motion detectors". The following chapter reviews the theoretical literature on motion detectors proposed for the visual system and discusses some experimental data from the auditory system which limits the choice of a detector mechanism. A plausible neural implementation for a acoustic motion-direction detector is suggested.

CHAPTER II

THEORETICAL CONSIDERATIONS

Based on the physiological finding that inhibition is involved in motion-direction sensitive neurons reported by Wagner and Takahashi (1990) only one particular model from the extensive literature on visual motion detection will be described here in more detail. The theoretical requirements that a detector sensitive to motion-direction requires two inputs which are processed differently and interact in a non-linear way, though, are satisfied by other models as well (see Borst and Egelhaaf, 1989).

The Barlow and Levick Model for Motion-Direction Sensitivity

In their classical paper, Barlow and Levick (1965) showed that directional selectivity in the rabbit's retina can be explained by an inhibitory mechanism. The response to the null direction is 'vetoed' by appropriate input from neighboring inputs (this is symbolized by the and-not gate in Fig. 6B). That is, the output from the inhibitory neuron 2 (see Fig. 6B) to the detector unit is delayed with respect to the output from the excitatory neuron 1 and/or temporally dispersed. If a stimulus moves through the receptive fields of neuron 1 and neuron 2 in the direction 1 to 2, the excitatory input from neuron 1 will cause the detector unit to fire and inhibition from neuron 2 will be too late to have a qualitative effect. In the opposite case - movement in the direction 2 to 1 - inhibition from neuron 2 reaches the detector almost simultaneously with the excitation from neuron 1, effectively canceling it.

The Biophysical Mechanism

The spread of electrical activity is one of the most important means of information processing in the brain. Neurons communicate via synapses, where "neurotransmitters" from the presynaptic cell cause the cell membrane of the postsynaptic cell to either depolarize or hyperpolarize by the opening of transmitter-gated ion channels (for an introduction, see Kandel et al., 1991). Usually, excitatory postsynaptic potentials (EPSPs) cause the cell to depolarize, inhibitory postsynaptic potentials (IPSPs) cause the cell to hyperpolarize. When the membrane potential, V, reaches are certain threshold, V_{thresh} by summating incoming activity from several sites over a certain amount of time, the cell responds by eliciting action potentials which propagate unattenuated to further cells. The action potentials (spikes), have a duration of about 1 ms.
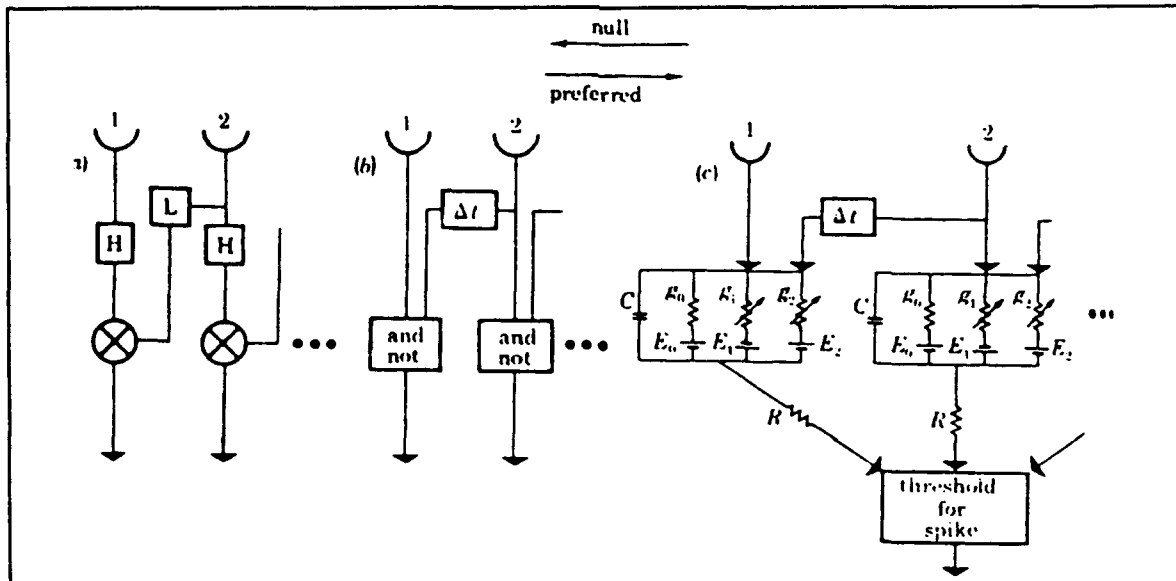
Fig. 6. Models for motion detection proposed for the visual system. (a) Hassenstein and Reichardt (1956). (b) Barlow and Levick (1965). (c) The model of Torre and Poggio (1978) can be used in a realistic simulation. [Taken from Torre and Poggio (1978)]

The current flow in a neuron can be modeled by an electrical equivalent circuit (Kandel et al., 1991) (compare Fig. 6C). The total of passive channels in the membrane

can be represented by a battery (E_0 in Fig. 6C) in series with a conductor (g_0). The membrane itself possesses a capacitance, C. Synapses are equivalent to batteries (E_1; E_2) in series with variable ("gated") conductances (g_1; g_2).

Torre and Poggio (1978) proposed a specific biophysical mechanism as the mechanism underlying the directional selectivity to motion. They showed that the interaction between the excitatory and the inhibitory synapse is highly nonlinear if the inhibitory equilibrium potential is close to the resting potential of the cell. They demonstrated in a lumped electrical model of the membrane that this "shunting inhibition" can cancel the excitatory postsynaptic potential induced by an excitatory synapse without hyperpolarizing the membrane (Fig. 6C). Details on how this mechanism is implemented in this model are given in Chapter III (Methods).

Specialty of the Auditory System

One aspect in which the auditory system is distinct from the visual system is the extension of the source: in the auditory world typically only point sources occur which, besides their location, may merely differ in the composition of the frequency spectrum. The architecture of the owl's ICc (Chapter I), suggests that the activity in this nucleus should allow to distinguish between a single object moving from one to a second location, and a new object appearing at that second location. This is because within ICc the sound spectrum is preserved as explained below. Since the location of a sound source is signaled by firing of several neurons in one of the ITD columns described above, acoustic motion will elicit firing of neurons in one column at time t_1 and firing of neurons in another column at time t_2. Which neurons respond in each column depends on the frequency spectrum of the object. If one assumes that the frequency spectrum of the moving object stays approximately the same, neurons firing at time t_2 will only be

considered to signal the same object as those firing at time t_2 if most of them lie in the same "frequency rows" as the ones firing at time t_1. The work by Takahashi and Keller (in press) actually suggests that the detection of a moving stimulus by neurons in the ICc is less influenced by background noise than the detection of a stationary stimulus.

Detectors of Change in Interaural Phase Disparities

For Wagner and Takahashi (1990) speculate that "motion-direction sensitive cells have the ability to preserve the spectrum of the moving sound" because these cells were found at several levels of the time pathway, the proposed model contains several local detectors of change in interaural phase disparities per frequency row of the ICc. Each detector unit works similar to the units proposed by Torre and Poggio (1978) (Fig. 6). With this arrangement, each detector can distinguish between a change in phase difference from $\Delta\Phi_1$ to $\Delta\Phi_2$ as opposed to a change in the opposite direction and hence signals a change in the horizontal position of the sound source. This answer is ambiguous since the neurons responding to $\Delta\Phi_1$ and $\Delta\Phi_2$ could also signal "phantom sources" (see Eq. 1). Inputs from the local "phase change detectors" signaling the same particular time difference change converge at a higher level (the output level in the model) on units whose response depends on the coherence of the frequency spectrum of the sound source. Presumably, the biological analogue to the connection between local detectors and the output units is be the projection from the ICc-ls to ICx (Knudsen 1984; Takahashi and Konishi, 1986; Wagner et al., 1987). It can be shown that for the static case ($v \rightarrow 0$) the inhibition does not play a qualitative role (Fig. 15), hence the output of the model can be taken as ICx output. As mentioned above, the interaction of the converging frequency channels appears to involve nonlinear processes (Takahashi and

Konishi, 1986). Although this process is not modeled in detail, the threshold of the ICx elements in the model introduces a nonlinearity (Fig. 16).

CHAPTER III

MATERIALS AND METHODS

Structure of the Model

General Outline

While acknowledging that an efficient computer model with many neurons can not take all aspects of single cells into account and although not much is known about cell properties in the owl's midbrain from intracellular recordings (Moiseff, 1985) the author believes that network models which claim biological relevance should not be built upon a oversimplified model of the neuron (Grzywacz and Amthor, 1989). The approach here follows Bower (Wilson et al., 1989) and others in trying to "reverse-engineer the brain with the objective of understanding the functional organization of its very complicated networks." This strategy of "computational neuroscience" (Sejnowski et al., 1988) differs from the "connectionist" approach (e.g. Rumelhart et al., 1986) in that it takes into account available experimental data and thus can evolve along with the experimental program (Sejnowski et al., 1988).

The model was constrained by anatomical and physiological data although some additional assumptions had to be made. The final model consists of three layers, each of which corresponds to a nucleus in the owl's midbrain. The layers are composed of simulated neurons (units) exhibiting responses similar to real neurons. There are 13 units in each frequency band; the output layers contains 13 broadly tuned units. For some simulations (e.g. Fig. 15) this model was replaced by a two layer model with direct

connections between input and output layer for efficiency. The following sections explain the single-cell model and the layer structure of the model.

Modeling of the Input Layer Neurons

The output of each unit in the input layer was modeled as a stochastic spike train that was modulated sinusoidally with ITD. The average maximal spike rate was set to 200 Hz in agreement with data presented by Fujita and Konishi (1991). The sinusoidal modulation in time was derived from the finding that neurons in the core of the inferior colliculus (ICc) which the model neurons are supposed to mimic, respond in a cyclic manner not only to ITD (Fig. 7) but also to continuously changing interaural phase difference, binaural beats (Moiseff and Konishi, 1981; Yin, 1983; Spitzer and Semple, 1991; Takahashi and Keller, in press).

For each frequency of the stimulus spectrum, the neuron in the column whose array specific ITD (see above) corresponds to the actual position of the sound source fires, as well as the neurons in columns whose common ITD differs multiples of the period - corresponding to the phantoms.

An example for a unit of the input layer is shown in Fig. 8. This unit is tuned to 3000 Hz and to an azimuth of 0 degree. The x-axis represents time, but the location the simulated sound source would be at a certain point in time is marked. In reality this source would start on the far left, then move to the far right and then return. The input neuron shown fires, whenever the "stimulus" passes through 0 degree azimuth. Units in the input layer do not have a built in motion-direction bias and since all simulations
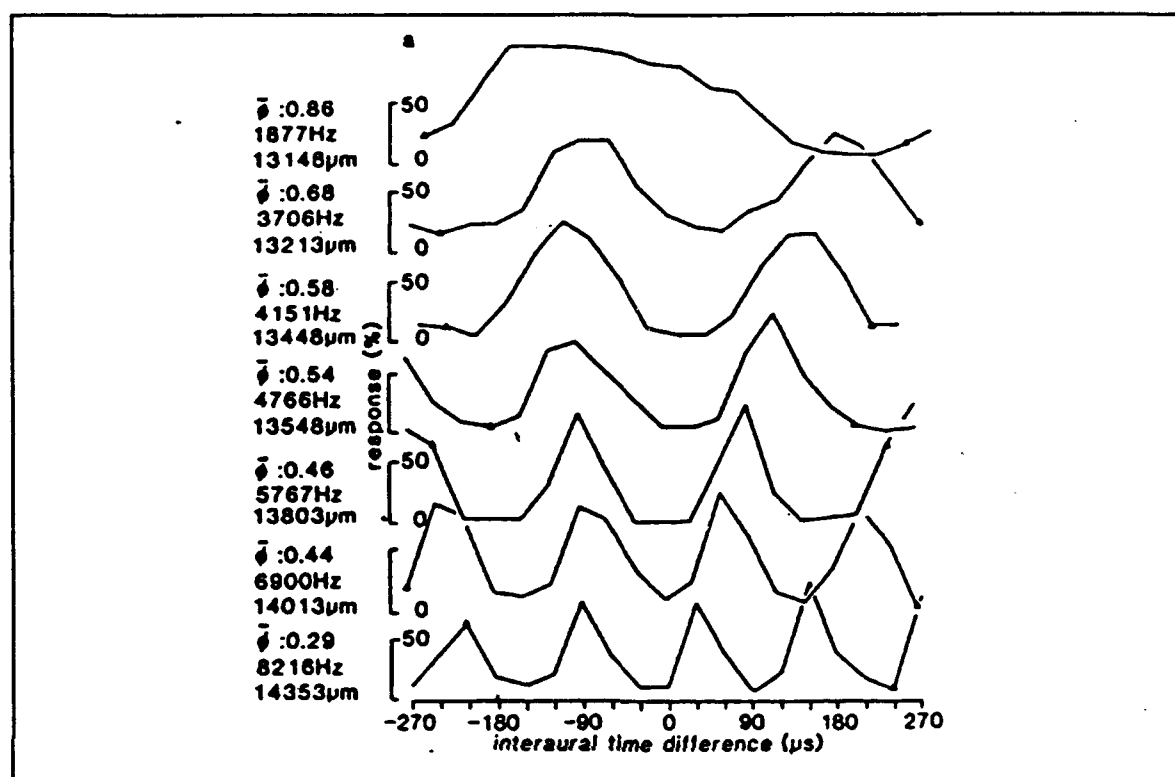
Fig. 7. Electrophysiological data from neurons of an array in the ICc. These response curves are modeled by sinusoids in the model (see e.g. Fig. 8). [Taken from Konishi et al. (1988)]

are averaged over 20 runs, do not show a bias.

Single Cell Model for the Middle and Output Layers

Analogous to anatomical data, neurons with different frequency tuning but signalling one ITD, the array-specific ITD (Wagner et al., 1987), converge onto one output layer neuron as symbolized in Fig. 5. There, spike trains feed onto "synapses" of elaborated "integrate-and-fire" model neurons as described below. For the middle and output layers an adaptation of a single-cell model is chosen which has been developed for visual cortex simulations by Wehmeier et al. (1989) and Wörgötter and Koch (1991). The neurons are treated as being iso-potential, lumping the dendrites and the axon into a single electrical

PSTH of ICc Neuron 6 (Jitter 0ms)
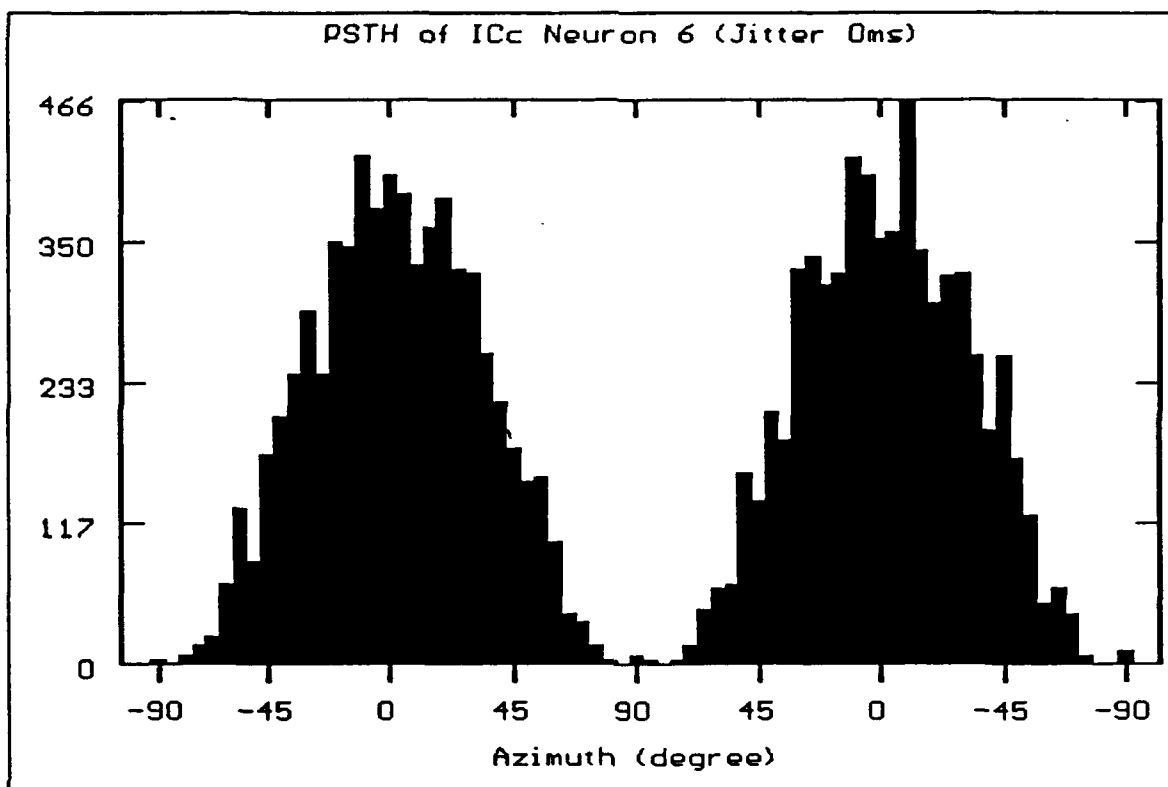
Fig. 8. Input layer unit, f = 6750 Hz, excitation = 50.

compartment with a physiologically plausible input resistance and a passive time constant $\tau = C/g_0$ (Segev et. al, 1989). The contribution of synapses is described by a time-varying conductance change g(t) in series with a synaptic battery (Fig. 6C). The action potentials, in real cells caused by fast, voltage gated Sodium and Potassium channels, are modeled as discrete, binary events. Preparatory experiments with a model that incorporated those channels revealed that the additional computational effort involved in this slows simulations down considerably and the adjustment of the parameters of the model such as the reversal potentials and the synaptic delays becomes very difficult (see also Yamada et al., 1989). The behavior of individual neurons is still reasonably physiological and sufficient for the model, although this might change as more data from intracellular recordings becomes available. The time course of the membrane potential

is then given by solving the following differential equation (compare with Wilson and Bower, 1989) which is solved using standard numerical methods (Mascagni, 1989) (for details see Chapter III, Computer Implementation).

$$C\frac{dV(t)}{dt} = \sum_{j=1}^{k} g_1(t-t_j)(E_1 - V(t))$$
$$+ \sum_{j=1}^{n} g_2(t-t_j)(E_2 - V(t)) + g_0(E_0 - V(t)) \tag{2}$$
$$+ g_{AHP}(t-t_{spike})(E_{AHP} - V(t))$$

The number of excitatory synapses, k, is one in most simulations; the inhibitory synapses, n, are those involved in the directional and lateral inhibition, respectively. The presynaptic action potential with arrival time t_j induces a conductance change given by an α function (Jack et al. 1983) with a time to peak (t_{peak}) of 1ms for excitatory and the directionally independent inhibitory connections and t_{peak} = 20ms for the directionally dependent inhibitory connections:

$$g(t) = g_{peak}\frac{t}{t_{peak}}\exp(1-\frac{t}{t_{peak}}) \tag{3}$$

Note that the resulting membrane potential is not necessarily the linear sum of the individual synaptic contributions to the somatic potential since synaptic conductance inputs interact nonlinearly (Rall, 1964; Torre and Poggio, 1981).

Organization of the Layers and Connections

The connection from the first to the second layer establishes the motion-direction sensitivity: units in the middle layer (presumably corresponding to ICc) receive excitatory in put from one cell in the input layer and inhibitory input from a neighboring cell in the input layer.

Units in the output layer receive excitatory input from all frequency bands of their best ITD in the previous layer. In most simulations, nine frequencies from 3000 Hz to 9000 Hz were used in the input and middle layer. There is no gain control mechanism built into the model, but weights are adjusted to get output in the same range for simulations run with different numbers of frequency channels.

A simplified version of this model contained only two layers for the sake of computational efficiency. In this version, one unit in the output layer received excitatory input from input layer neurons in different frequency bands and inhibitory input from their neighbors to one side. This version was used initially and is sufficient to account for the speed tuning (Fig. 15).

In both, the simplified and the enhanced version of the model, lateral inhibitory connections between units in the output layer could be installed. Taking into account physiological data by Knudsen and Konishi (1978b) (Fig. 2), inhibitory interaction with neighboring units decreases with distance and extends about 45° in each direction.

As mentioned above, the experimental data show that cells in ICc-ls as well as cells in ICx are sensitive to the direction of a moving sound source. To study how the DI depends on the temporal jitter of the signals in the individual frequency channels, the different frequency inputs were phase shifted relative to each other in a random fashion, examining different amounts of maximal jitter. The practical implementation of this phase shift which would correspond to different amounts of time for the computation of ITD in different frequency channels, was achieved by introducing delays in the connections between the middle and the output layer.

Simulation of the Motion-Direction Sensitive Unit

The intermediate (middle) layer contained the actual motion-direction sensitive units which are the above mentioned phase change detectors whose output fed to the output layer of the model. As every detector needs two inputs - that are neurons with neighboring receptive fields in this model - the distance between them, the sampling base, $\Delta\phi$ (Fig. 9), plays an important role. Since the actual input to the detector units consists of spatial sinusoids, Shannon's sampling theorem (Shannon and Weaver, 1949) demands a sampling base which is at most half the wavelength of the sinusoid to be processed. Theoretical (Götz, 1965) as well as experimental studies on movement-sensitive neurons in the cat visual cortex (Baker and Cynader, 1986) have found the optimal relation to be:

$$\frac{\Delta\phi}{\lambda} = \frac{1}{4} \tag{4}$$

In the model, a sampling base of 15° is used which is optimal for the higher range of frequencies (15° ≡ 30 μs ITD, hence $\lambda_{optimal}$ = 120 μs, that is a frequency of 8333 Hz). Judging from published graphs derived from theoretical calculations (Borst and Egelhaaf, 1989, their Fig. 3C) 3000 Hz, the lowest frequency used in the model, with $\Delta\phi/\lambda$ = 0.09, should still give a good response (Baker and Cynader, 1986, report a value of ~1/10 to 1/4 for the ratio $\Delta\phi/\lambda$).

Simulations (see also Pennartz and van de Grind, 1990; van Doorn and Koenderink, 1976) showed that the "realistic" approach used here doesn't allow for a pure delay of the inhibitory signal as originally proposed by (Barlow and Levick, 1965). As proposed by (Torre and Poggio, 1978), a leaky integrator which allows the inhibition to last longer
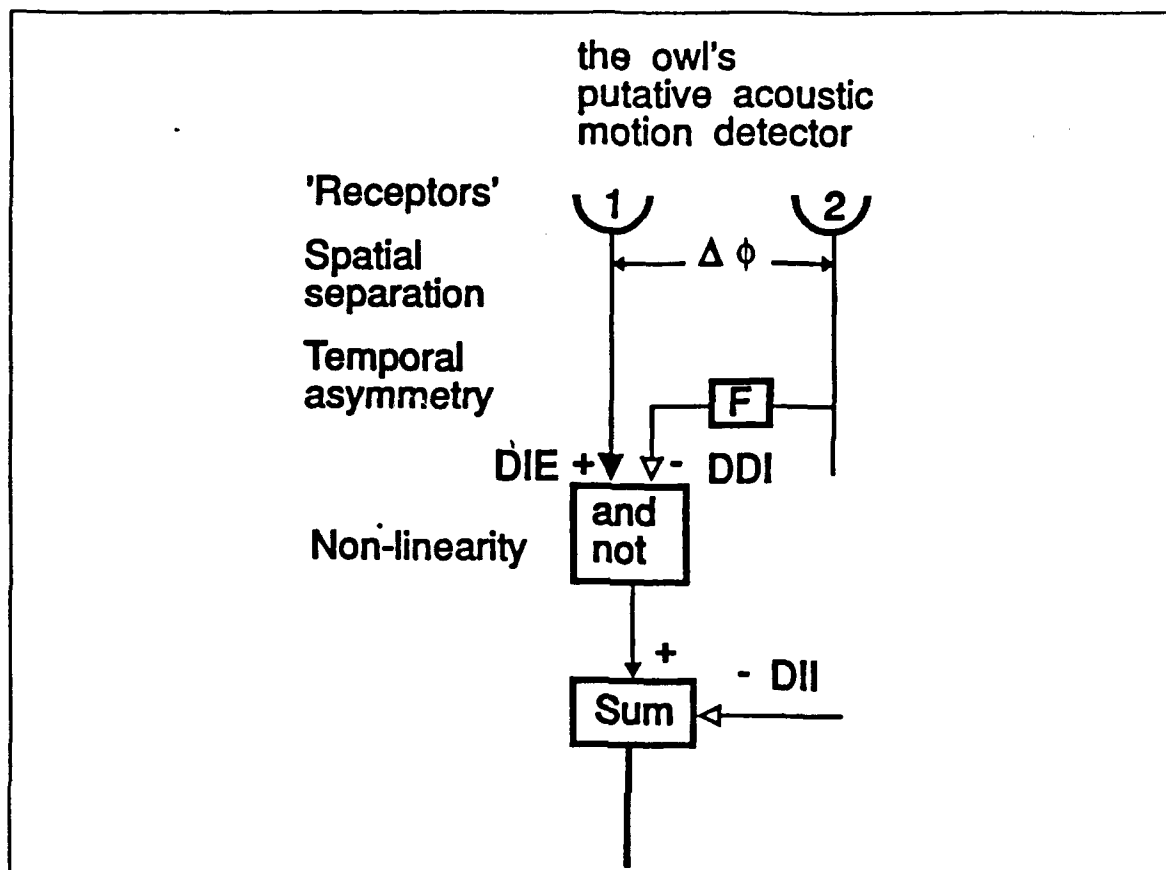
Fig. 9. The owl's putative acoustic motion detector. DDI: direction-dependent inhibition, DII: direction-independent inhibition, DIE: direction-independent excitation, $\Delta\phi$: sampling base. [Taken from Wagner and Takahashi (in press)]

than the excitation, is sufficient to achieve motion-direction sensitivity. This low pass filtering operation is implemented here with a longer time constant (t_{peak}, see Eq. 3) in the alpha function of the inhibitory conduction as compared to the excitatory conductance.

Computer Implementation

Simulations were performed on SUN Sparc-2 computers with a modified version of the general purpose simulator for biological neural networks, GENESIS (Wilson et al.,

1989). GENESIS is a graphically oriented, general purpose simulation system to facilitate the modeling of neural networks. It is designed specifically for use in simulation of biologically-based models on many levels of detail (Wilson et al., 1989; see also product reviews by Miller, 1990; and Plonski and Joyce, 1991). The authors envision that with widespread use of their simulator the comparison and evaluation of models reported in the literature will become easier in future - one of the reasons why this public domain simulator was used here.

The integration method used was a first-order exponential Euler numerical procedure, which is an explicit, stable method (for a review of the use of numerical methods in neuronal modeling, see Mascagni, 1989). A 100 μs time step allowed the simulation of 1.14 s of the complete model consisting of 117 input cells, 117 middle layer cells and 13 output cells with altogether 342 connections in ca. 6 hrs. The time step of 100 μs was adequate because the shortest interspike interval which could occur was 1 ms. Convergence was confirmed, however, by additionally using a time step of 10 μs on some runs, which yielded no significant difference, a method usually taken to be a rough estimate of convergence and stability (Mascagni, 1989). During the development of the model, numerous simulations were done to test building blocks and explore the parameter space. Since almost no intracellular recordings from the owl's midbrain exist, with the exception of an abstract by Moiseff (1985), parameters were taken from systems that have been better characterized. In particular, a parameter set also used by Wehmeier et al. (1989) seemed practical. The results are based on a large data set of simulations with the final set of parameters. For a typical simulation most parameters are set in two parameter files for cell, respectively layer constants. In preparatory runs some crucial variables could be set interactively and results were checked graphically with the use of the XODUS interface to standard X11 routines. For

larger simulations, a sequence was run from Unix shell scripts, without operator intervention.

Data Analysis

Most of the data analysis was done with the aid of script files in Mathematica (Wolfram Research), a flexible mathematical software packet. As one would do with physiological data, stimulus-locked poststimulus time histograms (PSTHs) were generated, the binwidth of which was $\frac{1}{72}$ th of the total time the stimulus needed to travel first clockwise, then counterclockwise. As commonly done in the literature, the directionality index

$$DI = 1 - \frac{response\ in\ null\ direction}{response\ in\ preferred\ direction} \qquad (5)$$

was used to characterize the motion-direction sensitivity of the modeled cells. Values near 0 indicate no difference in the response clockwise versus counterclockwise motion and increasing values indicate greater directionality.

CHAPTER IV

RESULTS

Fig. 10 shows the change of membrane potential (lower portion of Fig. 10) for a unit in the output layer as described above (Chapter III) as incoming signals arrive (upper portion of Fig. 10). The time course of the response of an output (ICx) cell for a stimulus moving first in the preferred direction and subsequently in the opposite (null) direction is shown. For this parameter combination (excitatory weights: 50 units; directional inhibition 1 unit) the model neuron behaves as expected from the earlier study by Torre and Poggio (1978). One can see that for the preferred direction almost every incoming spike from the input cell (upper trace in upper portion of Fig. 10) depolarizes the membrane whereas for the null direction, the effect of incoming spikes is suppressed by the inhibition from the neighboring input cell (lower trace in upper portion of Fig. 10) which now arrives almost at the same time as the excitation.

Input-Output Function of Single Cells

Fig. 11 and Fig. 12 show the input-output function of a single cell in the output layer of the model. Output spike rates are plotted against input rate of neurons in the input layer (Fig. 11) and weight of the connections between layers (Fig. 12). The response of cells to increasing input rates is approximately linear, at least for the range of connection weights used in the model (usually 50 units, see Fig. 11).
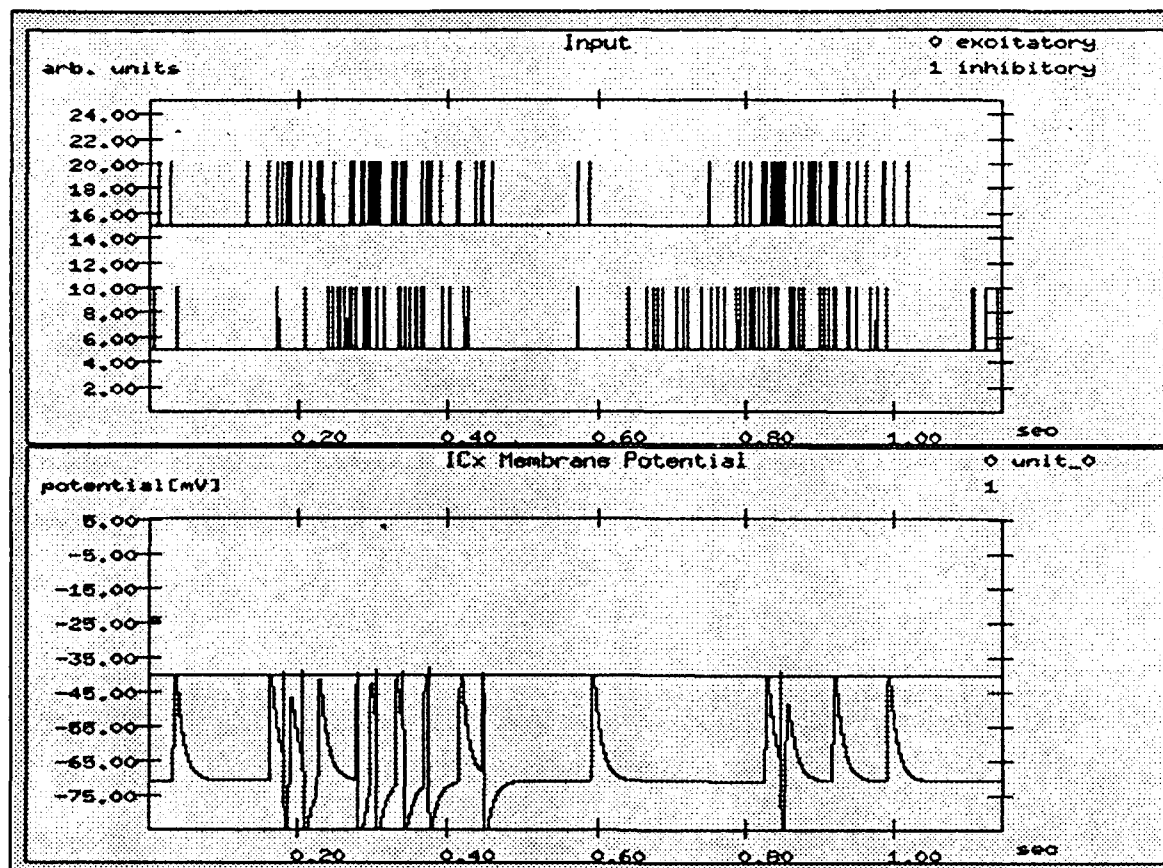
Fig. 10. Screen print of the change of membrane potential for an unit in the output layer as seen in the Xodus window of the GENESIS simulator. Clockwise motion (0..0.57sec) and clockwise motion (0.57..1.14sec) are shown in the same plot.

The Speed Tuning of the Proposed Motion Detector

It was known from the experimental data (Wagner and Takahashi, 1990) that the speed tuning curve of cells responding to motion had a shallow peak at 315°/s. Therefore, a time constant of 20 ms was chosen for the inhibitory conduction. This lead to a DI of about 0.5 with appropriate parameters for the excitatory (50 units) and inhibitory (1 unit) weights. With these parameters fixed, the speed of the simulated sound source was varied (Fig. 15). The results matched the experimental data fairly good. Note especially that the DI does not drop much for very high velocities. The results
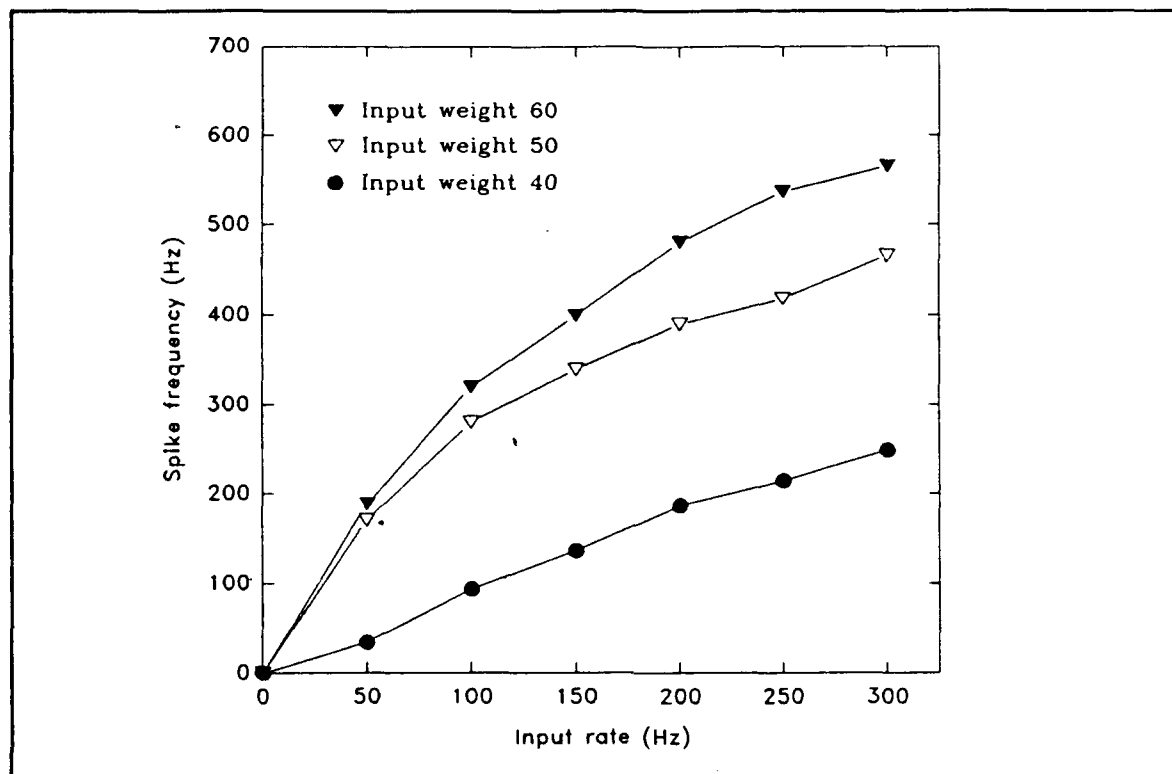
Fig. 11. Input-output function of a unit in the output layer (input from unit with f=3000Hz only). Dependence of spike rate on input rate for three different weights.

shown in Fig. 15 are from a simulation with two layers, however, simulations involving three layers did not show qualitatively different results. Adding lateral inhibition (see below) did not change the shape of the speed tuning curves.

In the framework of this model, one would interpret the broad speed tuning observed in the experiments as a consequence of the long time constants of the directional inhibition. Other interpretations, however, are possible; e.g. membrane properties. The decrease of the DI towards lower speeds is expected because for a slow moving stimulus needs the time needed to travel from one unit in the input layer to the next one is much greater than the time constants involved.
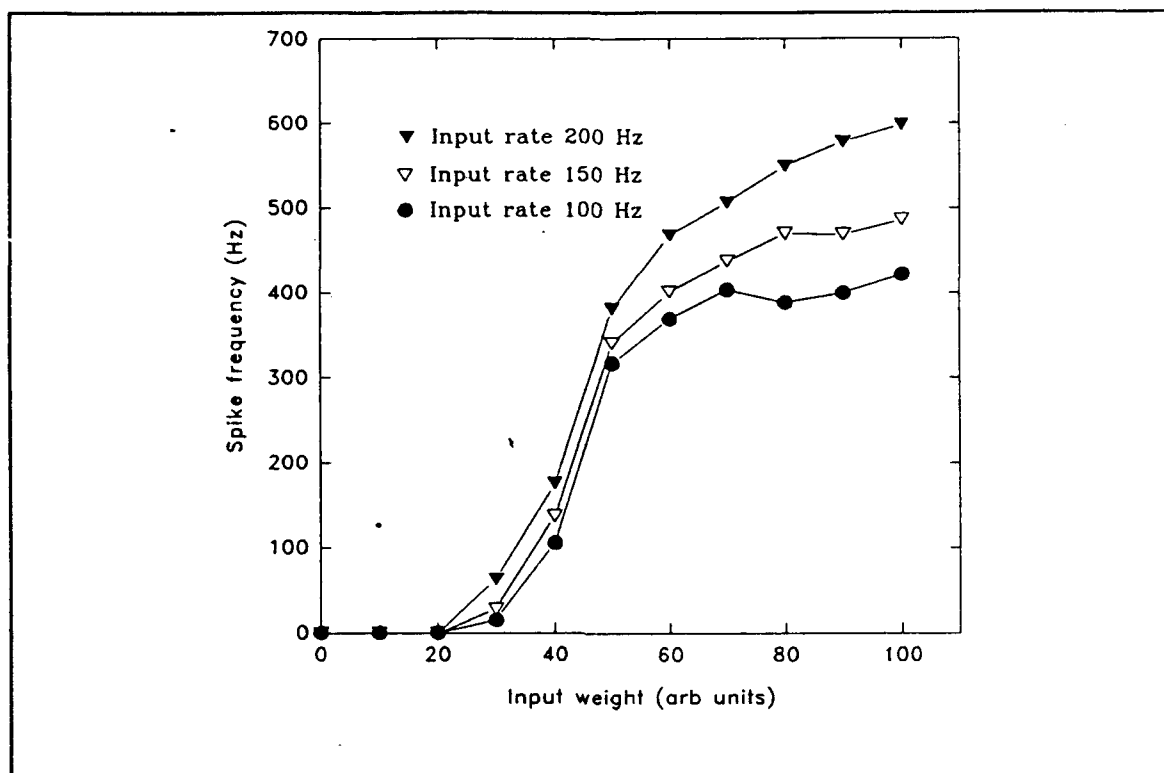
Fig. 12. Input-output function of a unit in the output layer (see Fig. 11). Dependence of the output rate on the input weight for three input rates.

The Influence of Channel-Convergence on Motion-Direction Sensitivity

Fig. 13 and Fig. 14 show qualitatively and Fig. 16 shows quantitatively that motion-direction sensitivity improves from the middle layer to the output layer (mean middle layer units (one location; nine frequency bands): 0.12; mean output layer units (locations 3-11): 0.49; Mann-Whitney U: $p < 0.01$). In Fig. 13 a unit tuned to a higher frequency ($f = 6750$ Hz) than the input unit shown in Fig. 8 is presented. Here, the unit not only responds to its characteristic interaural delay of $0\mu s$ but also displays sidepeaks multiples of the carrier frequencies wavelength apart. These peaks have about the same height for one direction, however, that is not the case for the output layer unit shown in Fig. 14 which clearly exhibits an enhanced peak at the ITD it is tuned to, in this case $0\mu s$.
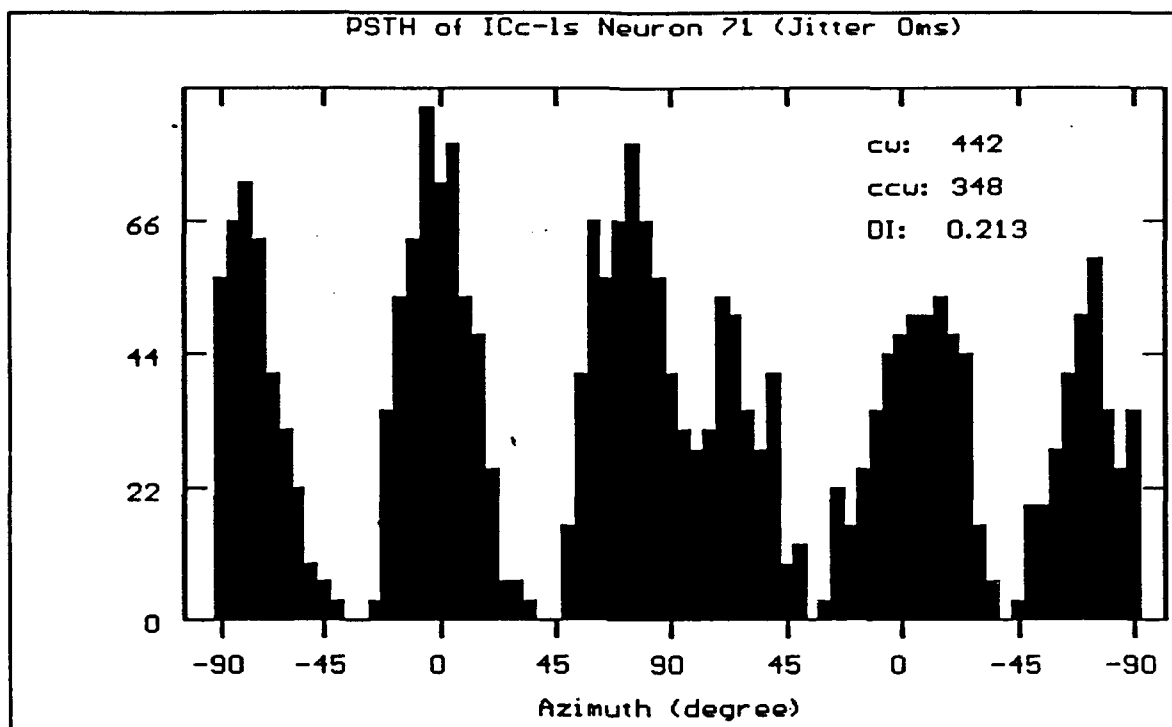
Fig. 13. Unit of the middle layer which shows motion-direction sensitive response. Frequency f = 6750 Hz.

The sidepeak suppression as well as the improvement in directionality are both due in part to the threshold function of the neurons which effectively causes a general reduction in neural activity. This effect can be further enhanced by lateral inhibition (see below).

Wagner and Takahashi (in press) have suggested that this "direction-independent inhibition" - which presumably is composed of single cell threshold and lateral inhibition between cells - is the second stage in a hypothetical, two-stage acoustic motion detector (Fig. 9).
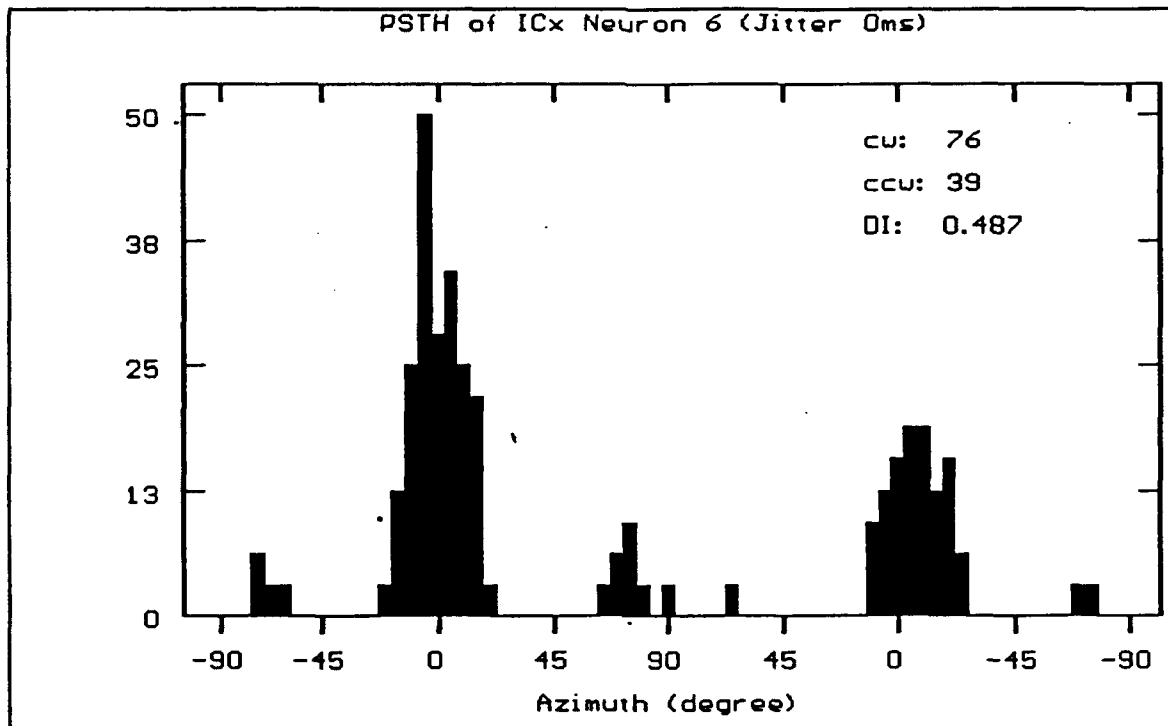
Fig. 14. Motion-direction sensitive unit (cw: clockwise; ccw: counter-clockwise) of the output layer which receives input from several units of the middle layer like the one shown in Fig. 13.

The Role of Lateral Inhibition

Determining the influence of lateral inhibition turned out to be difficult in the final, three layer model, because simulations showed inconsistent behavior for increasing lateral inhibition. It could be shown, however, that this was mainly due to the value of the weight between middle and output layer units. When this weight was set too low, lateral inhibition would not show a significant effect on the average DI of output layer neurons (e.g. without lateral inhibition, DI=0.49; with lateral inhibition, DI=0.52; Mann-Whitney U, p>0.1). Too low spike counts with this parameter combination caused too high deviations which even lead to an occasional negative DI (preferred direction: counter-clockwise instead of clockwise as normal because of the connections).
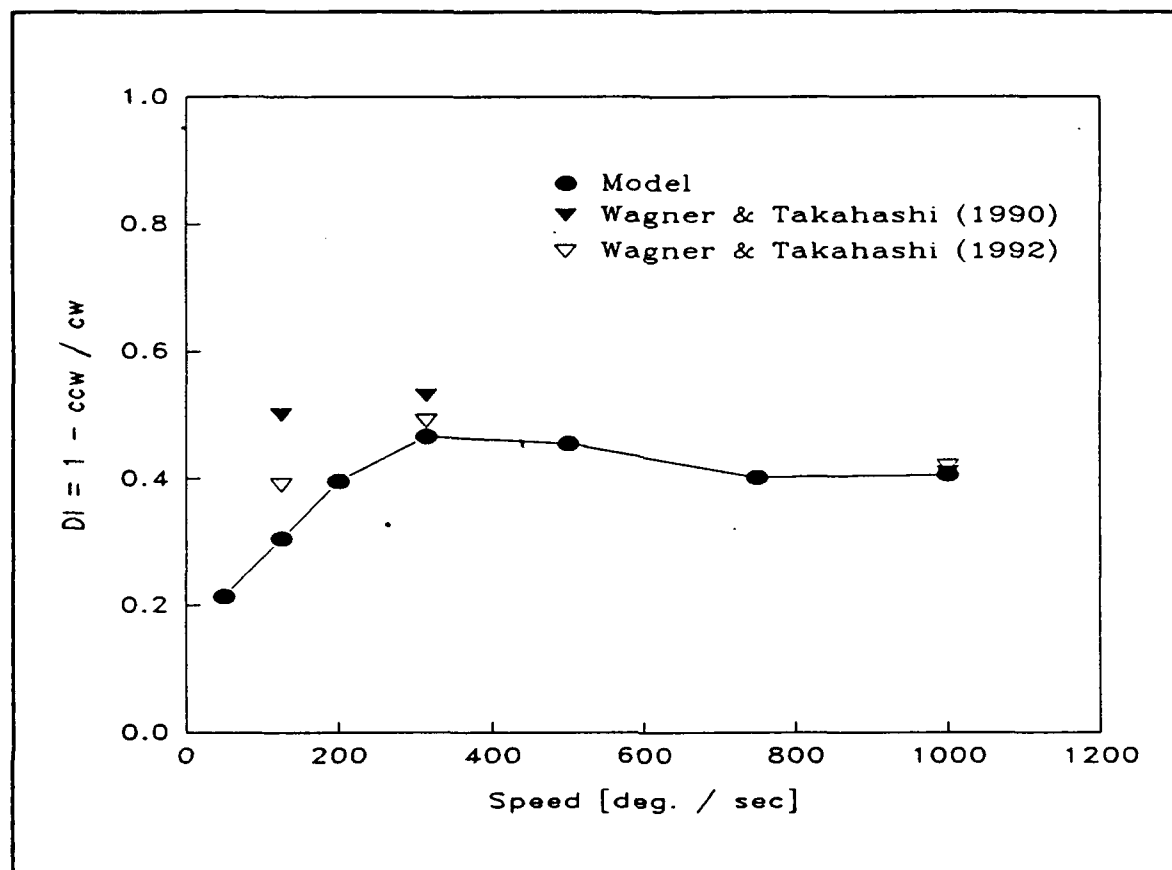
Fig. 15. Speed tuning of the model in comparison to experimental data (Wagner and Takahashi, 1990 and in press). Broad tuning is found in experimental and simulation data (simplified model, τ_{inh}=20ms; see text).

Increasing the weights between middle and output layer lead to a overall decline in directional sensitivity due to increased spike rates, but showed clearly the importance of lateral inhibition under these conditions: Fig. 17 shows the small, but significant increase of DI when the inhibition is introduced (without inhibition, DI=0.08; with inhibition, DI=0.22; Mann-Whitney U, p<0.01).

Lateral inhibition has been shown to play a major role in shaping the receptive fields of neurons in the auditory nuclei of the barn owl (Knudsen and Konishi, 1978c; Fujita and Konishi, 1991). In the case of stationary sound sources, Fujita and Konishi
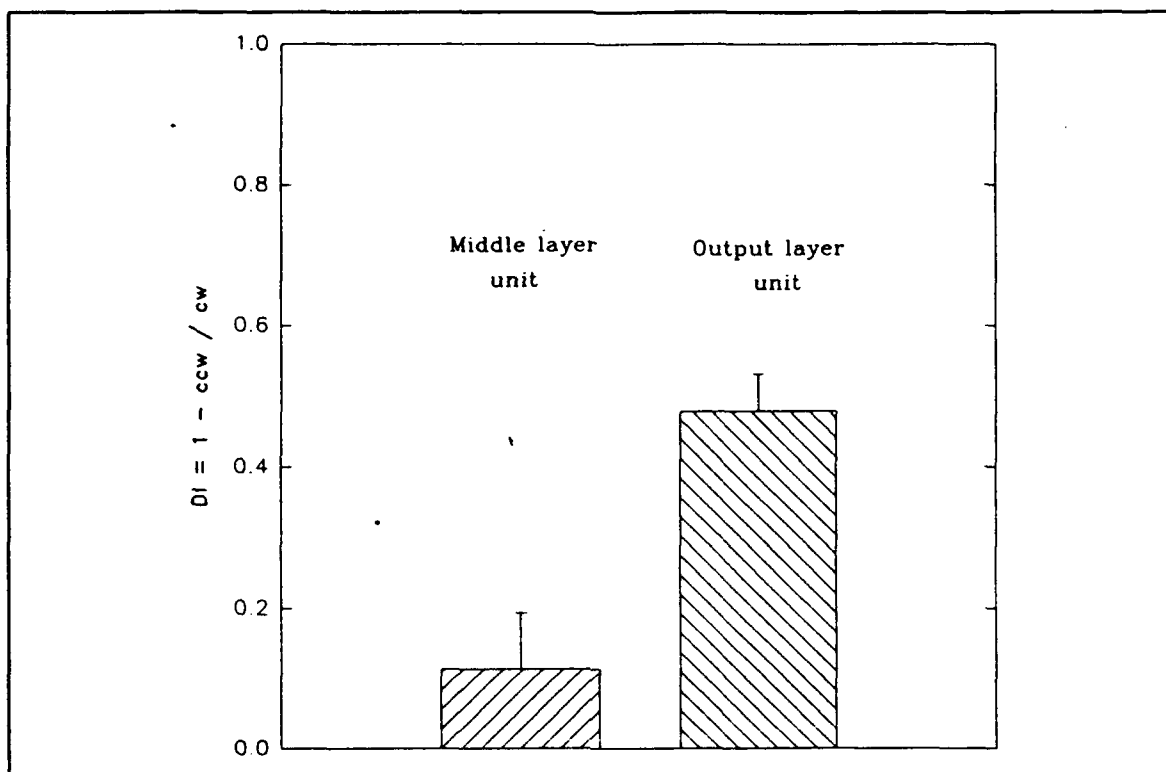
Fig. 16. Comparison of middle (n=9) and output (n=9) layer units with respect to motion-direction sensitivity.

(1991) showed that iontophoresis of bicuculline, an antagonist to the inhibitory neurotransmitter $GABA_A$ decreased the ITD selectivity in ICc and ICx neurons. The studies by Takahashi and Keller (in press) indicate that lateral inhibition also plays a role in the sharper tuning of ICc cells for moving stimuli.

The Effect of Jitter on Motion-Direction Sensitivity

As explained in Chapter III, jitter was introduced to find out about constraints the projection between ICc-ls and ICx has to obey in order to preserve motion-direction information. Intuitively, it seemed clear that phase-jitter would lead to a markable decrease of directional sensitivity in the output layer, but that turned out not to be the case. Instead, due to the long time constants of inhibitory synapses involved, the

60
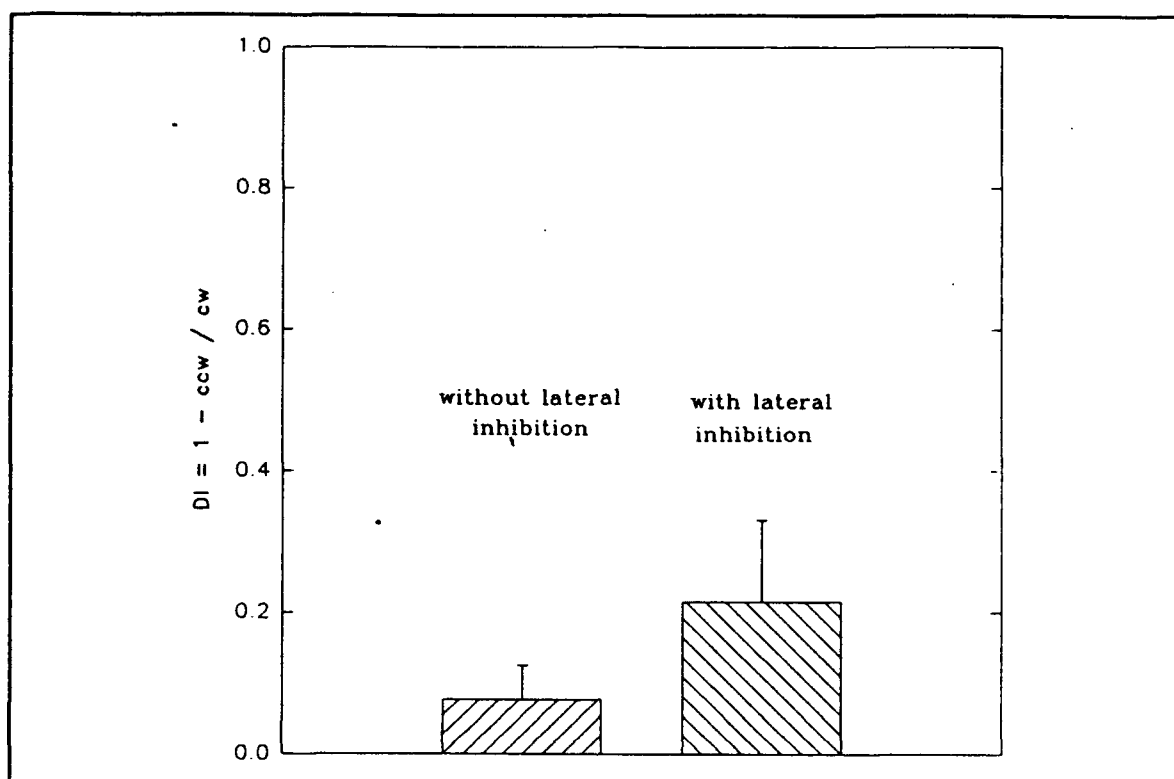
Fig. 17. The influence of lateral inhibition on the DI of output layer neurons. (Speed: 500°/s; data from 9 units, each with 20 repetitions)

decrease in sensitivity was not statistically significant.

The computations thus indicate that much of the anatomical jitter which might exist in the actual neuronal network disappears in the integrating process the neurons are performing.

CHAPTER V

DISCUSSION

The aim of this study was to better understand the neural mechanisms underlying the perception of auditory motion. Using ideas from the vision literature and the available neurophysiological data from a particular animal model, the barn owl, it has been shown that certain response properties of neurons in the owl's midbrain sensitive to motion-direction, in particular the speed tuning (Fig. 15) and the hypothesized improvement of motion-direction sensitivity in (at least) two stages, could be simulated with a "realistic" model system.

An improvement in motion-direction selectivity from one processing level to the next has been found by Levick et al. (1969) for direction-selective neurons in the rabbit lateral geniculate nucleus. Their Fig. 1B allows the estimate of an approximate 20% increase of the DI. Snowden et al. (1992) reported a greater directionality for neurons in the cortical visual area MT than for neurons in the preceding area V1. To propose such a model for the auditory system of the owl thus is reasonable in the light of the data presented here, which show that convergence and high thresholds naturally result in an improvement of directionality.

Validity of Assumptions

The connections between input and middle layer which establish the motion-direction selectivity may not be as direct as assumed in the current model. Instead,

another (excitatory) principal cell and an interneuron would perhaps be more plausible. However, the results presented here do not directly depend on this detail.

On a related issue, Shamma (1989) has noted that forward inhibition can be replaced by recurrent inhibition without qualitatively changing the results.

The single cell model (Chapter III) makes only very general assumptions, but since neither cell properties nor the place on the cell, where the computations take place, is known exactly, lumping the electrical properties of a neuron in a one-compartment equivalent model might indeed be too simple.

Other Models

Quite a few models have been proposed for motion detectors in the visual system. The first theoretical papers (Hassenstein and Reichardt, 1956; Reichardt, 1961; Marr and Ullman, 1981) have led to an still ongoing discussion (Reichardt, 1987; Hildreth and Koch, 1987; for a recent review, see Borst and Egelhaaf, 1989). A realistic model (for a definition, see Sejnowski et al., 1988) which is somewhat similar to the model presented here is explored in some depth by Pennartz and van de Grind (1990). So far, nobody has given a complete account for motion-direction sensitivity in the auditory system, although there are scattered suggestions in the literature (Wagner and Takahashi, 1990 and in press; Takahashi and Keller, in press). Some aspects of the auditory system of the barn owl have already been subject to computer modeling studies (Pearson et al., 1990; Grün et al., 1990; Brainard et al., 1992; Sullivan, 1990).

This is probably the case for most of the so-called "connectionist networks", which are currently very popular in the cognitive sciences. It might be interesting, though, to test some of the ideas presented here in the framework of a model for the barn owl inferior colliculus, recently developed for a different study by Fleming, Goodwin and

Takahashi (personal communication) which uses standard backpropagation algorithms to train a two-layered network to represent two targets simultaneously. Backpropagation has indeed already proven to be useful in training "realistic" neural networks for predicting interneuronal connectivity from input-output information, see, e.g., the work by Zipser and Andersen (1988), Lehky and Sejnowski (1988, 1990). In a recent review, Lockery (1992) makes the interesting claim that a model by Lockery et al. (1989) has actually proven that it is "feasible to train synaptic connections in networks of multicompartmental model neurons" and proposes the use of "hybrid models" (Lockery, 1992).

The finding that the circuit's overall design, broad receptive fields and long inhibitory time constants serves to relax the anatomical precision with which it need be wired, is comparable in principle with the results of Freed et al. (1992) who found that various sources of "jitter" in the anatomical circuit for a model of a ganglion cell in the cat's retina are smoothed by the use of broad-field elements as input.

Experimental Implications

Some of the assumptions underlying the model could, in principle, be experimentally tested (e.g. the value of the sampling base introduced in Chapter III), and parameters (e.g. inhibitory time delays) could be determined experimentally. The results of this study furthermore suggest experiments which could be useful to determine the nature of the computational mechanism involved in motion-direction sensitivity.

Sillito (1977) reports a reduction of direction selectivity during iontophoretic application of bicuculline, an antagonist of the inhibitory neurotransmitter $GABA_A$. This might be difficult to show in this system, though, because the release from inhibition will also lead to a decrease in the ITD selectivity in ICc and ICx neurons (Fujita and Konishi,

1991). Nevertheless, the model would predict that release from inhibition in motion-direction sensitive neurons would generally decrease the DI. However, increase in inhibition (e.g. by applying the inhibitory neurotransmitter $GABA_A$) might not always lead to an increase in DI, if firing rates are lowered too much.

Also, the negative results of trying to influence the motion detection system by phase shifting input in different frequency channels relative to each other, could be tested. The simulations predict a very robust behavior of the motion-sensitive neurons in that the DI does not change significantly even with appreciable "jitter" in the input.

Suggestions for an Extension of the Model

As more physiological data becomes available, the model can be expanded and adjusted in several ways. Most interesting would be a better account of intracellular properties of the different neurons involved in the network. This would allow a more elaborated model of single cells, e.g. in adding some kind of dendritic branching. It would be interesting to try to include the "evidence for a computational distinction between proximal and distal neuronal inhibition" (Vu and Krasne, 1992; Koch et al., 1982) in the model although at this time there is no experimental data on this in the owl.

Two main extensions of the model are evident: on the one hand, the model will have to be extended to two dimensions (so far, nothing is known about the coding of the third dimension); on the other hand, the clustering of neurons of a particular preferred direction will be an interesting topic.

Wagner (1992 and personal communication) has experimental evidence for the existence of so-called "motion columns", all neurons within which uniquely code for one direction. Albright (1984) showed motion columns for the visual area MT of the macaque.

The simulations demonstrate the usefulness for such "motion columns" in the auditory system of the owl in at least the lateral shell since convergence of neurons coding for different directions would decrease the directional response in the output layer, the presumed ICx.

Conclusion

A "realistic" model of some aspects of the neural network in the owl's inferior colliculus which is responsible for sound localization and motion detection was presented. It could be shown that a few plausible assumptions made the replication of data from electrophysiological experiments possible. The feasibility of such an approach for modeling auditory computations was demonstrated. With more knowledge about intrinsic properties of the neurons involved and the connections between them it will be possible to build a more complete and sophisticated model of the neural computations which underlie the fascinating behavioral abilities of the barn owl. Modeling studies such as the thesis presented here might be helpful not only to better understand the computational processes involved but also to guide the experimental work and provide explanatory frameworks to aid in the integrative interpretation of experimental data. The code used in the simulations has been made available for the GENESIS user group based at Caltech and might become useful for other applications, too.

APPENDIX A

THE SCRIPT PROGRAM FOR THE GENESIS SIMULATOR

NOTE: This file does not show the whole program, instead, it shows how the construction of the layers and the connection between them is done in the script language of GENESIS and presents some core routines.

```
/                                                              /
=============================================================
//              The IC external nucleus (space map)
/                                                              /
=============================================================

enable /tpcell
create neutral /ICx
createmap /tpcell /ICx \
    {ICx_NX} {ICx_NY} {ICx_SEPX} {ICx_SEPY} \
    {min_ICxX} {min_ICxY}
disable /tpcell
echo ICx (output) layer constructed

//===========================================================
//                  lateral inhibition in ICx
//===========================================================
region_connect /ICx/tpcell[]/axon to \
    /ICx/tpcell[]/soma/inh_syn with synapse -rel \
    1 1 \                        /* one positive source region   */
    {min_ICxX} {min_ICxY} \   /* max. source region */
    {max_ICxX} {max_ICxY} \    /* xmin,ymin,xmax,ymax */
    2 1 \                        /* one pos. destination region  */
    {-2.6*ICx_SEPX} {min_ICxY} \   /* 7 cells as    */
    { 2.6*ICx_SEPX} {max_ICxY} \   /* destination region      */
    -1 \                         /* one neg. destination region  */
    {-0.4*ICx_SEPX} {min_ICxY} \   /* no self inhibition !   */
    { 0.4*ICx_SEPX} {max_ICxY}
expweight /ICx/tpcell[]/axon \
    {ICx_ICx_weight_decay} {ICx_ICx_inh_weight} {minimal_weight}
set /ICx/tpcell[]/axon:@/ICx/tpcell[]/soma/inh_syn \
```

```
          delay {ICx_ICx_inh_delay}
set /ICx/tpcell[]/axon:@/ICx/tpcell[]/soma/AHP \
          weight 10.0


//=============================================
//                The mathematical input layer (ICc ls)
//=============================================

enable /cell
create neutral /ICc
createmap /cell /ICc \
          {ICc_NX} {ICc_NY} {ICc_SEPX} {ICc_SEPY} \
          {min_ICcX} {min_ICcY}
disable /cell
echo ICc (input) layer 1 constructed
enable /tpcell
create neutral /ICcls
createmap /tpcell /ICcls \
          {ICc_NX} {ICc_NY} {ICc_SEPX} {ICc_SEPY} \
          {min_ICcX} {min_ICcY}
disable /tpcell
echo ICc (input) layer 2 constructed


//=============================================
//                Connections between layers
//=============================================

  for(x = 0 ; x < ICc_NX ; x = x + 1)          /* all positions      */
    for(y = 0 ; y < ICc_NY ; y = y + 1)        /* all frequency bands */
      str indexstr = {x+y*ICc_NX}
      str element = "/ICc/cell[" + {indexstr} + "]"
      str ICclselement = "/ICcls/tpcell[" + {indexstr} + "]"
      connect {element}/axon to \
              /ICcls/tpcell[{x+y*ICc_NX}]/soma/exc_syn with synapse
      connect {ICclselement}/axon to \
              /ICx/tpcell[{x}]/soma/exc_syn with synapse
      if(x > 0)
       connect {element}/axon to \
              /ICcls/tpcell[{x+y*ICc_NX-1}]/soma/inh_syn with synapse
       set {element}/axon:@/ICcls/tpcell[{x+y*ICc_NX-1}]/soma/inh_syn \
              delay {ICc_ICcls_inh_delay} weight {ICc_ICcls_inh_weight}
      end
    end
  end
// Setting the axonal propagation velocity
radialdelay /ICcls/tpcell[]/axon -uniform \
     {ICcls_ICx_exc_delay_zero} {ICcls_ICx_exc_delay}
set /ICcls/tpcell[]/axon:@/ICcls/tpcell[]/soma/AHP \
     weight 10.0
set /ICc/cell[]/axon:@/ICcls/tpcell[]/soma/exc_syn \
```

```
      weight {ICcls_ICx_exc_weight*ICc_NY}
set /ICcls/tpcell[]/axon:@/ICx/tpcell[]/soma/exc_syn \
      weight {ICcls_ICx_exc_weight}

adjustspike


//=================================================
//                  Repeat motion maxrep times
//=================================================

int rep
for(rep = 1 ; rep < 21 ; rep = rep + 1)        //10 reps to make statistics better
  reset                                         //before setting files
  echo repetition: {rep}              '


//=================================================
//            input to the mathematical layer (here: cw, higher spk rate)
//=================================================
int showflag2=1
  for(x = 0 ; x < ICc_NX ; x = x + 1)           /* all positions      */
    for(y = 0 ; y < ICc_NY ; y = y + 1)         /* all frequency bands */
      str indexstr = {x+y*ICc_NX}
      str element = "/ICc/cell[" +{indexstr}+"]"
      float BF = {min_frequency+d_frequency*y}
      float BITD = {min_ITD+d_ITD*x}
      set {element}/sin mode 0 \           /* sine */
          amplitude {INPUT_rate} \       /* gets divided by 2 in source code */
          dc_offset {INPUT_rate/2.0} \ /* no negative spike rates */
          phase {90.0-(180+BITD)*1e-6*360*BF} \ /* sin->cos,180=0deg */
          frequency {1e-6*BF*vel_us_ITD_per_sec}
    end /* for x */
    int showflag2=1
  end   /* for y */


  for(y = 0 ; y < ICc_NY ; y = y + 1)
              str indexstr = {6.0+y*ICc_NX}
              str elementicc = "/ICc/cell[" +{indexstr}+"]"
              set {elementicc}/monitor file_io 1 interval_fname icc{indexstr}_{num}cw
              str elementmid = "/ICcls/tpcell[" +{indexstr}+"]"
              set {elementmid}/monitor file_io 1 interval_fname mid{indexstr}_{num}cw
    end

  for(x = 0 ; x < ICx_NX ; x = x + 1)
      str indexstr = {x}
      str element = "/ICx/tpcell[" +{indexstr}+"]"
      set {element}/monitor file_io 1 interval_fname icx{indexstr}_{num}cw
  end
```

```
//================================================
//        start the simulation (via graphics or autom.)    -- cw --
//================================================
  check      .
  status -process
  int mem={status(-memory)}
  if(mem > 134217728)
    quit
  end
  step -t {tmax}
```

APPENDIX B

CONSTANTS FOR UNITS AND LAYER

These are constants used in the single-cell model:

```
randomseed  -new              // initialize the random # generator

float       PI          =     3.14159

// channel equilibrium potentials    V
float       Eexc   =    20.0e-3        //excitatory synaptic reversal potential
float       Einh   =   -71.0e-3        //inhibitory synaptic reversal potential
float       Eleak  =    -71.0e-3       //leakage potential
float   EAHP    =   -90.0e-3       //afterpolarization reversal potential

// peak channel conductance
float   Vex    =   exp(1.0)        //scaling factor
float       Gexc   =   Vex * 0.011e-6 //S
float       Ginh   =   Vex * 0.055e-6  //S
float   GAHP    =   Vex * 0.59e-6    //S

//time to peak for all conductance changes
float   tpeak   =   1.0e-3         //sec
float   tpeak_exc   =   1.0e-3        //sec
float   tpeak_inh   =   20.0e-3       //sec

//spiking threshold
float   phasic  =   0.07
float   tonic   =   0.1
float   Vthresh =   -40.0e-3    //V
```

The following are some constants and variables used in the simulations

```
//======================================================
//              general simulation specific parameters    (dk)
//======================================================
float   PI       =      3.14159
float default_binwidth =   .095        //95ms on-on-time

// setting the simulation clocks
float   dt       =   0.0001   //sec per time step
float refresh_factor = 1.0
setclock        0 {dt}          // sec   '
setclock        1 {dt * refresh_factor} //sec
setclock        2 {default_binwidth}  //default

randomseed -new

//======================================================
//              IC specific parameters      (dk)
//======================================================
float min_frequency     =       3000.0
float max_frequency     =       9000.0
float d_frequency       =       750.0
float max_ITD           =       180.0                   //usec
float min_ITD           =       -180.0          //usec
float d_ITD             =       30.0 //usec, determines # of cells
                                //should be 1/4 of lambda
                                //see Goetz, 1968


//======================================================
//              layer specifications (dk)
//======================================================

// specifications for ICc - the first layer of cells
int     ICc_NX = { (max_ITD-min_ITD)/d_ITD+1}
                // number of cells in x direction  - mediolateral - IPD
int     ICc_NY = round( { (max_frequency-min_frequency)/d_frequency+1} )
                // number of cells in y direction  - dorsoventral - frequencies
float   ICc_SEPX = 1.0
float   ICc_SEPY = 0.0
float   ICc_SEPZ = 0.0
float   min_ICcX = {-(ICc_NX-1) * ICc_SEPX/2.0}
float   max_ICcX = {(ICc_NX-1) * ICc_SEPX/2.0}
float   min_ICcY = 1.0                   //so that (ICcY-ICxY)^2=1
float   max_ICcY = 1.0

int     ICx_NX = ICc_NX
int     ICx_NY = 1                       // integrates over all frequencies
```

```
float   ICx_SEPX = ICc_SEPX
float   ICx_SEPY = ICc_SEPY
float   ICx_SEPZ = ICc_SEPZ
float   min_ICxX = {-(ICx_NX-1) * ICx_SEPX/2.0}
float   max_ICxX = {(ICx_NX-1) * ICx_SEPX/2.0}
float   min_ICxY = {-(ICx_NY-1) * ICx_SEPY/2.0}
float   max_ICxY = {(ICx_NY-1) * ICx_SEPY/2.0}


//=======================================================
//                    run time parameters
//=======================================================
float   on_on_time = {default_binwidth}
float   vel_degree_per_sec = {30.0/on_on_time}          //see W&T 1990
float   vel_us_ITD_per_sec = {2.0 * vel_degree_per_sec}   //2us per degree
float   delta_t_per_cell   = .{d_ITD/vel_us_ITD_per_sec}
float   tmax = {360.0/vel_us_ITD_per_sec}     // -90 to 90 degree
float   binwidth = {delta_t_per_cell}
setclock 2 {binwidth}          // note: clock for file output set to time window of psth
setclock 9 {getclock(2)}       // for graphics
str     testmode = "n"
int     GRAPHICS = 0
int     max_INPUT_rate = 200   //(Hz);  see Fujita and Konishi, 1991

// setting the weights for connections btw layers

float   ICc_ICcls_exc_delay    = 0.0
float   ICc_ICcls_inh_delay    = 0.0
float   ICc_ICcls_inh_weight = {0.0}
float   ICc_ICcls_inh_delay = 0

float   ICcls_ICx_exc_weight_min = {50.0}
float   ICcls_ICx_exc_weight_max = {60.0}
float   ICcls_ICx_exc_weight_step = {10.0}

float   ICcls_ICx_exc_delay = 0 //2ms estimated
float   ICcls_ICx_exc_delay_zero = 0.0
float   ICcls_ICx_exc_delay_min = {0.0*delta_t_per_cell}
float   ICcls_ICx_exc_delay_max = {0.0*delta_t_per_cell}
float   ICcls_ICx_exc_delay_step = {0.5*delta_t_per_cell}

float   ICx_ICx_inh_weight_min = {0.0} //give 9spks with exc 20
float   ICx_ICx_inh_weight_max = {1.5} //give 9spks with exc 20
float   ICx_ICx_inh_weight_step = {0.5} //give 9spks with exc 20

float   ICx_ICx_weight_decay = {-0.1/ICx_SEPX}
float   ICx_ICx_inh_delay  = 0.0
float   minimal_weight = 0.0     //default - used for lat inh
```

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The influence of temporal cues on acoustic motion-direction sensitivity of auditory neurons

in the owl

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lemniscus

Summary and conclusions

1. We studied the sensitivity of auditory neurons in the barn owl's brainstem to the direction of apparent acoustic motion. Motion stimuli were generated with an array of seven free-field speakers (Fig. 2). Motion-direction sensitivity was determined by comparing the number of spikes elicited upon movement in the counter-clockwise (CCW) direction with the number of spikes recorded upon clockwise (CW) motion. A directionality index (DI) was defined to quantify the measurements. The statistical significance of the directional bias was determined by a χ^2-test that used the responses to stationary sounds as the null hypothesis.

2. Neurons sensitive to the direction of motion were found in many nuclei of the auditory pathway such as the nuclei of the lateral lemniscus, the inferior colliculus (IC), and the optic tectum (OT) (Figs. 3, 5, 6-10).

3. In the majority of motion-direction sensitive neurons (71%) the response in the preferred direction was equal or less than the response to stationary sound. On the other hand, the response in the null direction was lower than the response to stationary sound in almost all neurons (94%).

4. Velocity tuning was broad (Fig. 6). In the sample of 33 cells a shallow peak appeared around 310 deg/s within the range tested (125 - 1200 deg/s).

5. A silent gap between the bursts from successive speakers caused a decrease in motion-direction sensitivity. This decrease was linear with gap duration, and also depended on the apparent velocity (Figs. 7, 8, 10, 11).

6. The velocity dependence disappeared, if the change of motion-direction sensitivity was plotted as a function of the duty cycle, which was defined as (duration of a burst from a speaker - rise/fall time of a burst)/interstimulus interval) (Figs. 10, 11).

7. For the population of neurons tested, motion-direction sensitivity decreased as the neural activity increased (Fig. 12).

8. A two-stage scheme including a direction-independent excitation, a direction-independent inhibition, and a direction-dependent inhibition is proposed as a hypothetical acoustic motion detector (Fig. 13). The properties of this detector are compared with those of visual motion detectors.

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these mechanisms, it is instructive to consider some of the well-studied motion-detection

schemes that have been proposed for the visual system (Fig. 1; Reichardt 1961; Barlow and

Levick 1965; Borst and Egelhaaf 1989).

Fig 1 was here

Each of the models requires two spatially separate receptors. In the auditory system

of the owl, neurons with spatial receptive fields, the space-specific neurons, have been

reported. Such neurons may be regarded as the equivalent of the receptors in the models.

The space-specific neurons are arrayed in the external inferior collicular nucleus (ICx)

according to the position of their receptive fields such that a retina-like map of sound

source locations is formed (Knudsen and Konishi 1977). The discrete spatial receptive fields

of these neurons are generated by selectivity for interaural differences in time (ITD) and

intensity (ILD), the binaural cues for the localization of targets in the horizontal and vertical

planes, respectively (Knudsen and Konishi 1979; Moiseff and Konishi 1981; Moiseff 1989;

Olsen et al. 1989). The space-specific neurons obtain inputs from two different neural

pathways, termed the time and intensity pathway, respectively, because neurons in these

pathways are sensitive for one of the binaural cues, ITD or ILD, but not the other (Moiseff

and Konishi 1983; Takahashi et al. 1984).

The time-shift between the two inputs may be an absolute delay, for example due to

a delay line. Such a delay would be independent of the stimulus parameters. A fixed time-

shift was incorporated in some models of visual motion detection (Fig. 1a, b). On the other

hand, the time-shift may depend on stimulus parameters like the temporal frequency (Fig.

1c), and such time-shifts may be represented by filters like a low pass.

Having described the basic properties of the motion detectors, we shall briefly

explain how these detectors work. Thus, referring to the model depicted in Fig. 1a, if a

stimulus moves from left to right, the excitatory impulses from receptor 1 arrive at the non-

linear interaction stage before the inhibitory impulses from receptor 2. The earlier arrival

allows them to pass this stage and elicit an excitatory response at the detector level. On the

other hand, if a stimulus moves from right to left, the inhibitory impulses of receptor 2,

which are triggered earlier, will be delayed, and, if receptor 1 is stimulated with

approximately the same delay as is implemented in the neural connections, will block or

'veto' the response at the detector level. Since rightward motion causes a strong response it

is termed the preferred direction of this motion detector, while leftward motion that causes

no (or a weaker) response is termed the "null" direction. The other models behave in

basically the same way, except that the non-linear interaction of the two responses at the

detector level differ. Some models use a facilitation (Fig. 1b, c) that may be formalized as a

logical 'and' gate (Fig. 1b) or as a multiplication (Fig. 1c).

Materials and methods

Twelve, adult, captive-bred barn owls were used in the experiments. All

experiments were performed under anaesthesia (Ketamine, 20 mg/h/kg). Diazepam (Valium;

1mg/h/kg) was given as a relaxant, and Atropin sulfate (0.05 mg/kg) was used to prevent

salivation. Surgery was performed according to aseptic standards. At the beginning of an

experiment a stainless-steel head plate was fixed to the animal's skull. For this operation,

the anaesthetized animal was placed in a stereotaxic head-holder that fixed the head such

that the plane defined by the center of the ear bars and the ventral surface of the palatine

ridge was tilted 45 degrees downwardly from the horizontal plane. The head plate was fixed

to the skull with dental cement and a reference post was glued onto the skull at the

intersection of the interaural axis and the midline of the skull.

For the following electrophysiological experiments, a skin incision was made over

the dorsal surface of the skull, and part of the dural surface was exposed through a

craniotomy. All recordings were made in an anechoic chamber (3mx3mx3m). A heating pad

warmed the animal throughout the experiment. Glass-coated platinum-iridium electrodes

were positioned with respect to the reference post and advanced through the brain from

dorsal to ventral with a remote-controlled stepping motor. Single and multi units were

recorded in different nuclei. For the anatomical identification of the recording sites small

electrolytic lesions (+2 μA DC, 10s) were made in some cases. After an experiment, the

craniotomy and skin incisions were closed, the wound treated with an antibiotic creme, and

the animal was placed in an observation cage. Owls did not show any signs of discomfort

after recovery, and ate normally on the day after an experiment.

Stimuli: Two different stimulus paradigms were used. During the search phase dichotic stimuli were presented with stereo earphones (Sony MDR-E 272 or Aiwa HP-V17). Stimuli were bursts of broad-band noise or tones with a duration of 100 ms duration and rise/fall times of 5 ms, generated with a Wavetek Model 132 signal generator and a custom-built electronic switch and amplified with a commercial power amplifier (Yamaha AX-300 or Yamaha AX-730). The response of the neurons to changes in the ITD (ITD-curve) or the ILD (ILD-curve) was recorded into computer memory (IBM AT).

The motion stimuli were generated by seven free-field speakers (Mac Audio, *Fig 2 was here* ML103E, 10 cm speaker, bandwidth: 50 - 18000 Hz) arranged in a horizontal semicircle at 1 m distance from the owl (Fig. 2a). Speakers were placed at 30 deg intervals from +90 deg (owl's right, speaker #1) to -90 deg (owl's left, speaker #7). The height of the semicircle was variable. The array of speakers was activated in a 'roundtrip' pattern that simulated a source moving either first in the counter-clockwise (CCW) and then in the clockwise (CW) direction or first CW and then CCW. Stimuli from the individual speakers consisted of noise bursts (flat between 1 and 25 kHz) having a 5 ms rise/fall time and durations from 10 ms to 245 ms. The apparent velocities ranged from 125 deg/s to 1200 deg/s. The duration of the stimuli, the interstimulus interval (ISI) which determines the apparent velocity of the motion, and the overlap or silent interval ("gap") between successive sounds (Fig. 2) were controlled by a computer (IBM AT). We shall speak of a complete overlap of the stimuli from the individual speakers, if the successive activation caused no changes in sound level. Note that, due to the rise/fall transients, the gap assumes a negative value (-rise/fall time) in this case. Note also that only two of the three variables can be varied independently. Neural responses were recorded 10-50 dB above the threshold of a neuron.

Apart from the variation of the temporal parameters, several different stimulus conditions were used:

condition 1:   all speakers sequentially activated, apparent movement first CCW, then CW,

condition 2:   all speakers sequentially activated, apparent movement first CW, then CCW,

condition 3:   the most effective or 'best' speaker activated twice with the time interval between activations corresponding to that of condition 1,

condition 4:   the most effective or 'best' speaker activated twice with the time interval

between activations corresponding to that of condition 2.

The first two conditions represented the motion conditions; the latter two conditions were the stationary conditions.

The time of action potentials, relative to the onset of the roundtrip, was recorded in computer memory and analyzed as peristimulus time (PST) histograms. The PST-histograms were divided into two halves for analysis. One halve consisted of the sum of all spikes elicited while the stimulus was moving CCW, and the other halve consisted of all the spikes recorded while the stimulus was moving CW. In some neurons an onset response was seen (for example Fig. 5c, e), and those responses were excluded from the analysis. The directional sensitivity of the responses was quantified with a directionality index (DI):

$$DI = 1 - \frac{\text{lower spike count}}{\text{higher spike count.}} \tag{1}$$

"Lower spike count" and "higher spike count" refer to the halves of the PST-histogram with the lower and higher number of spikes, respectively (Figs. 3 - 7). For some analyses this unsigned DI was used (Fig. 12), but most time the DI was signed, so that positive values were assigned to neurons with a preferred direction in the CCW direction, and vice versa. Neurons showing no preference for a direction have a DI around zero, and neurons with a strong directional preference have a DI close to 1. Note that the DI per se confers no information about the statistical significance of a response, because a maximal DI would result if 1 spike is measured upon stimulation in the preferred direction while no spike is measured upon stimulation in the null direction. Care was taken to avoid artifacts due to low spike numbers by accepting only those responses that contained at least 10 spikes in the preferred direction. To judge the statistical significance of the DI, we compared, using a χ^2-test, the halves of the PST-histogram from trials recorded with conditions 1 and 2 with those from trials recorded with conditions 3 and 4. Since in the one-speaker tests, there was no spatial separation of the two sequential stimuli, a symmetrical response, i.e. the same number of spikes in the first and second halve was expected. Thus, these conditions represented the null hypothesis for the χ^2-test. In those cases in which no one-speaker test was performed, the mean of the response in the CCW and CW directions was used as null

hypothesis in the χ^2-test. This was always done to test for a bias in the one-speaker test. Two cells were biased when tested with the one-speaker conditions and were excluded from the further analysis. Since the one-speaker tests typically resulted in a slight bias which was due to the statistical variance of the response, two χ^2-tests were carried out. The numbers representing the null hypothesis were exchanged between the two tests, and, as a further safeguard against biases, only those units were accepted as motion-direction sensitive that showed significance (p<0.05) in both tests.

Anatomy. After the experiments with an animal were finished, the owl was deeply anaesthetized with an overdose of pentobarbital (Nembutal, 30mg) and perfused with 4% paraformaldehyde. Brains were blocked stereotaxically and placed in 30% sucrose until they sank. Thirty-micron thick frozen sections were cut on a microtome. Sections were stained with cresylviolet or Luxol-Fast-Blue (Du Pont solvent blue 37). Camera-lucida drawings were made from the sections and the position of the lesions was reconstructed.

Results

Since we were interested in motion-direction sensitivity in azimuth, we searched for neurons that were sensitive to ITD. After a cell was identified we switched from dichotic stationary stimulation to the free-field motion stimulation. For this study recordings were made at 295 sites, and in 211 of the recordings motion stimuli were presented. Some two-thirds of the recordings were from single units; for the rest more than one neuron contributed to the recorded response. The responses at 61 of the 211 sites were motion-direction sensitive as demonstrated by the χ^2-test. Multi and single unit recordings resulted in similar motion direction-sensitivity. From other dichotic experiments it was already known that ITD-sensitive neurons have a very low spontaneous activity, and more than 95% of the spikes were due to an excitation caused by the stimulus (Wagner 1990).

Many neurons in the auditory system are motion-direction sensitive

The basic tests to assess the motion-direction sensitivity were usually conditions 1, 2, and 3 or 4 at 95 ms ISI (Figs. 3, 4). Motion-direction sensitive neurons showed an increased response in either CCW (Figs. 3a, b, 5a, b, d, e, 6) or CW directions (Fig. 5c, f) which was independent of the two test conditions (Fig. 3a, b). In some cases, asymmetries with respect to conditions 1 and 2 were observed, i.e. a higher directional sensitivity with either condition 1 or condition 2 occurred. These asymmetries were due to an onset effect superimposed upon the motion-direction effect. However, they had no influence on the changes of the response induced by changing the temporal structure of the stimulus.

As may be seen in Fig. 3a, the neuron responded more when the stimulus moved in the CCW than when it moved in the CW direction. With condition 2 (Fig. 3b) it could be demonstrated that the lack of a response in the CW direction is not due to an adaptation of the response after the initial response in the CCW direction. The one-speaker test (condition 3, Fig. 3c) finally showed that the response became symmetrical if a stationary stimulus was presented, and *this also argues against adaptation as an explanation for the asymmetry in the* histogram of Fig. 3a. Such behavior was typical for all neurons. The χ^2-test in this neuron revealed a high directionality ($\chi^2=25.6$, p<0.001). In contrast, a neuron that was not motion-direction sensitive ($\chi^2=1.25$; p>0.05) (Fig. 4), would give the same response in CCW and CW directions, and would do so for the motion as well as the stationary conditions.

Motion-direction sensitive responses could be obtained from different nuclei throughout the brain. The lowest hierarchical level that was examined were the nuclei of the lateral lemniscal complex, and motion-direction sensitive responses were found there (Fig. 5a). There were also motion-direction sensitive cells in the core of the central nucleus of the inferior colliculus (ICc-core) (Fig. 5e), the lateral shell of the central nucleus of the inferior colliculus (ICc-ls) (Fig. 5c), and the external nucleus of the inferior colliculus (ICx) (Fig. 5f). Further upstream, motion-direction sensitive neurons were detected in the optic tectum (OT) (Fig. 5d).

The range of motion-direction sensitivity can be seen by comparing Figs. 3a, b, 5c, 5e, 6a, b (high DI) with Figs. 5b, d, f (intermediate DI) and with Fig. 5a (low DI). Due to

the limited data base at some anatomical levels we cannot state whether motion-direction sensitivity increased from the hierarchically lowest nucleus to the higher nuclei. Most often a single speaker dominated the response (Figs. 3, 5c, e, and 6). However, in some instances, a larger proportion of the speakers elicited a response when activated in the preferred direction than when activated in the null direction (Figs. 5a, f). In these cases, the motion-direction sensitivity resulted from a reduced response in the null direction to stimulation from one or more speakers that were effective in the preferred direction. In still other examples, both a response to more speakers in the preferred direction as well as a marked higher response upon stimulation in the preferred direction from the most effective speaker contributed to the motion-direction sensitivity (Fig. 5b, d).

Since all these neurons are embedded in neural maps of ITD, one might speculate that the total phenomenon we describe is due to lateral interactions in the network upon the stationary responses of the neurons. If this would be correct, the motion-direction sensitivity should change when the owl is rotated relative to the speaker array, because a rotation changes the relative contributions from the individual speakers. If the receptive field is centered in the middle of two speakers in the array, motion-direction sensitivity would disappear. Different signs of the motion-direction sensitivity should be measured, if the receptive-field center is first positioned to the right of the best speaker and afterwards to the left of the best speaker. Although the rotations changed the receptive-field center from one side of the original 'best speaker' to the other, a change in the sign of the directionality index was never seen. In addition, after initial recordings, the 'best' speaker was often properly centered in the receptive field of a neuron. Upon this repositioning no obvious changes in the directionality index were observed. This also rules out undersampling by stimulating from 'only' 7 free-field speakers.

Velocity dependence of motion-direction sensitivity

The velocity dependence of motion detectors must be band-pass shaped because the detector will not be able to respond in a directionally sensitive way for very low and very

high velocities. It follows that there will be a maximal directional sensitivity in a middle

range of velocities. The response of many visual motion detectors is tuned to velocity in just

this way (Barlow and Levick 1965; Borst and Egelhaaf 1989). The optimal velocity depends

on the delays in the interaction of neighboring inputs (Fig. 1). Neurons were tested with

apparent velocities ranging from 125 deg/s (240 ms ISI) to 1200 deg/s (25 ms ISI). Since in

many cells slow velocities elicited more spikes than high velocities, care was taken that

enough spikes were accumulated for the calculation of the DI for all velocities. In the

example depicted for Fig. 6 the DI was high for all velocities, suggesting that these velocities

Fig 6 was here

were near the optimal velocity of the detector. Note that in this example the response with

even the highest velocity is concentrated within some 50 ms, indicating that this neuron can

react precisely to very short sounds and also to sounds from rapidly moving sources. Thirty-

three neurons were tested with three different velocities and a complete overlap of the

stimuli from the individual speakers. The mean values and standard deviations of the DIs

(>900 deg/s: 0.42+/-0.23; 310 deg/s: 0.49+/-0.20; 125 deg/s: 0.39+/-0.24) demonstrated a

moderate dependence on the apparent velocity. Since for most neurons the response to the

middle velocity had the highest DI (see also Fig. 10a, b), the basic tests were conducted at

this apparent velocity.

Decrease of motion-direction sensitivity with gap duration

The introduction of silent intervals tended to diminish the motion-direction

sensitivity. Such gaps may influence motion-direction sensitivity if the interaction between

the two channels has some temporal limitations. Since many neurons stopped responding

immediately after stimulus offset, during a gap no neural response can accumulate that could

contribute to the motion-direction sensitivity. Thus, this stimulus situation is different from

the one in which velocity was changed but no silent interval appeared (Fig. 6). The routine

test was to compare the DI obtained with the 30 ms ISI and 35 ms duration with the DI in

the condition with 240 ms ISI and 35 ms duration. Thus, in these two paradigms the

stimulus duration was the same, but they differed in that the former contained no silent

interval, while during the latter stimulus sequence, a gap of 210 ms occurred between the

activation of successive speakers. The mean value of the DI in the latter test was 0.12, which is less than one third of the mean value obtained with the former paradigm, and in only one of 26 cells was the motion-direction sensitivity measured with the latter paradigm higher than the motion-direction sensitivity measured with the former paradigm.

This finding could be substantiated with other gap durations. The examples presented in Fig. 7 represent selected cases of the neurons whose response without a gap was shown already in Figs. 3, 5, and 6. For example, the response shown in Fig. 7b was obtained with a gap of 60 ms from the neuron shown also in Fig. 3. While in the situation of complete stimulus overlap, only a response from one speaker, and only upon motion in the CCW direction could be elicited (Fig. 3a, b), after the introduction of a gap, a response could be elicited from several speakers (Fig. 7b). In this as well as other neurons, the introduction of a gap also led to an increased response at the most effective speaker for motion in the null direction, so that without knowledge of the response without a silent interval, the preferred direction often was no longer obvious: compare Fig. 3 with Fig. 7b. These findings were common in all other neurons, 3 more examples of which are shown: the response in Fig. 7a was obtained with a gap of 71 ms from the neuron already shown in Fig. 5e. Fig. 7c demonstrates how a gap changed the response of the neuron also shown in Fig. 5d, and Fig. 7d shows the effect of a gap in the neuron shown in Fig. 6.

Fig 7 was here

The change of the DI with gap duration had a number of underlying causes (Fig. 8). In phasic neurons, like the one shown in Fig. 5e, the systematic increase of the gap resulted in an almost linear increase of the neural activity in the null direction, while the response in the preferred direction remained unchanged (Fig. 8a). In some neurons, a decrease of the spike numbers in the preferred direction was accompanied by an increase in the spike numbers in the null direction (Fig. 8d). A change in the DI could also be achieved by a decrease of the neural activity in both directions (Fig. 8c), or by a decrease in the activity in the preferred direction accompanied by an almost constant response in the null direction (Fig. 8b).

Fig 8 was here

Independent of the changes of spike number with gap duration, a linear decrease of the signed DI with gap duration was seen in all neurons that preferred the CCW direction (Fig. 9a-c). The opposite held for neurons preferring the CW direction (Fig. 9d). Note that

Fig 9 was here

both directions of changes indicated a decrease of directional sensitivity with gap duration. The highest DIs were usually found in the situation when complete overlap of the stimuli from the individual speakers occurred. This phenomenon was seen for both apparent velocities tested (125 deg/s: Fig. 9b, d, Fig. 10a, b; 310 deg/s: Fig. 9a, c, Fig. 10a, b).

Relation between gap duration and directionality index is velocity dependent

It was mentioned above that the temporal properties of the visual motion detectors are determined by the time-shift between the inputs to the detector. In some models (Fig. 1a, b) the time-shift was assumed to be constant, while frequency dependent time-shifts were incorporated in other models (Fig. 1c). The change in DI with gap duration allowed us to test whether the lateral interaction is due to a constant or a frequency-dependent time-shift between two (or more) interacting inputs. If the time-shift were constant, the slope of the regression line between DI and gap duration should be independent of the apparent velocity. Figures Fig. 10a, b, and 11a show that this was not the case. Thus, DI depended on velocity when there was a gap. In all cases tested with both velocities, the absolute value of the slope of the regression line was smaller with the slower apparent velocity than with the faster apparent velocity (see Fig. 10a, b for two examples). The distribution of the slopes of the regression lines were overlapping, but clearly shifted (Fig. 11a). The difference was highly significant (U-test, N_1=23, N_2=20, $\hat{z}$=4.48, p<0.001). The mean values of the slopes were -0.948 for 95 ms ISI and -0.363 for 240 ms ISI. Interestingly the quotient of these means (0.384) is almost identical to the quotient of the apparent velocities (0.396). This indicates that both apparent velocity and gap duration play a role in computing acoustic motion-direction. What is changed in parallel in both cases is the relative contribution of the stimulus duration during a stimulus cycle. This relation is known as the duty cycle. The duty cycle was defined here as:

$$\text{Duty cycle} = \frac{\text{duration} - \text{rise/fall time}}{\text{ISI.}} \qquad (2)$$

Indeed it was found that the changes of the signed DI with the duty cycle were

almost identical with both velocities. This was obvious from the examples: in Fig. 10 c and d

the slopes calculated for the different apparent velocities are much more similar than in Fig.

10 a and b, respectively. It became even clearer if the distributions of the slopes of the

regressions lines were plotted (Fig. 11). If the slopes were calculated with the duty cycle as

the independent variable (Fig. 11b), the two distributions were indistinguishable (U-test,

$N_1=23$, $N_2=20$, $\hat{z}=1.28$, p>0.05). The mean values calculated from these distributions were

-0.90 for 95 ms ISI and -0.88 for 240 ms ISI.

Evidence for inhibition

During stationary stimulation only neurons representing one spatial location are

stimulated. Thus possible lateral interactions do not influence a neuron's response. The

situation is different during the motion conditions, because neurons representing different

spatial loci are then sequentially activated. The responses to stationary and moving sounds

were compared by using the responses occurring at the best speaker. The response to

stationary stimulation was at least 10% higher than the response in the preferred direction in

51% of the neurons, while in only 29% of the neurons the response in the preferred direction

was at least 10% higher than the stationary response. The respective numbers for the null

direction are 94% and 2%. Thus, in most neurons (71%) the response in the preferred

direction was not higher than the response to stationary sounds, while in almost all cases

(94%), the response in the null direction was lower than the response to stationary stimuli.

From this observation two types of inhibition could be deduced. The general reduction of

the responses in the motion conditions compared to the stationary conditions, detected in 51%

of the neurons, suggested the existence of a direction-independent inhibition. In addition,

when comparing stationary and motion conditions, the response was more reduced upon

motion in the null direction than upon motion in the preferred direction. This is most

clearly illustrated in Fig. 3. This observation suggested the existence of a second type of

inhibition, one that was active in a directionally selective way. Further evidence for such a

direction-dependent inhibition can be seen in the responses shown in Fig. 8a. In this neuron

the response in the preferred direction was independent of gap duration, while the response in the null direction increased with gap duration. The increase of the response in the null direction with increasing gap duration indicates a release of inhibition.

Motion-direction sensitivity decreases with increasing neural activity

The neurons with a motion-direction sensitivity in the upper range were those that responded phasically, i.e. with only one or two spikes upon stimulation in the preferred direction. These neurons often did not respond at all when the stimulus moved in the null direction (Figs. 3, 6). In fact, a tonic response to dichotic stimulation was often an indication that a neuron would show no motion-direction sensitivity. If, for the complete sample of direction-sensitive neurons, the DI of a neuron was plotted as a function of its activity, a negative relation resulted (Fig. 12). The important finding of Fig. 12 is that no entries occur in the upper right region of the diagram. Similar dependences were detected if only the spikes elicited upon stimulation in the preferred direction or only the spikes elicited upon stimulation in the null direction were plotted on the x-axis.

Discussion

Many neurons in different nuclei of the auditory system of the owl were sensitive to the direction of apparent motion of a sound source. The horizontal motion direction-sensitivity showed a broad velocity tuning. The introduction of a gap led to predictable changes in the motion-direction sensitivity that were dependent on both the apparent velocity and the gap duration, and could best be explained as a function of the duty cycle. In the following discussion we shall first compare our data with those of others, then discuss possible neural mechanisms underlying acoustic motion-direction sensitivity in the owl, and finally make some remarks on the behavioral relevance of our findings.

Motion-direction sensitivity in the auditory system

Motion-direction sensitive neurons were found in many different nuclei of the owl's auditory system. This is in agreement with earlier studies in mammals, that showed the existence of motion-direction sensitive neurons in the inferior colliculus (Schlegel 1980; Yin and Kuwada 1983), the superior colliculus (Rauschecker and Harris 1989), the auditory cortex (Altman and Kalmykova 1986) and the cerebellum (Bechterev et al. 1975). For the owl, as well as for other animals, it is not known whether the proportion of neurons showing motion-direction sensitivity or whether motion-direction sensitivity changes with the hierarchical level in the auditory system.

Upon changes in the temporal parameters, neurons from all nuclei followed the same rule: with increasing gap duration, motion-direction sensitivity decreased. We mainly recorded neurons in the owl's time pathway, i.e. those nuclei that contain neurons tuned to the ITD. In addition to the motion-direction sensitivity all these neurons also showed some positional sensitivity. The detection of positional sensitivity begins at the level of the nucleus laminaris, that is located at a hierarchically lower level than the nuclei we probed (Moiseff and Konishi 1983). It is not known whether laminaris neurons show motion-direction sensitive responses. Such responses were, however, not found in the medial superior olive, the nucleus of mammals that is analog to nucleus laminaris (Yin and Chan 1990). Thus the motion-direction sensitivity may be computed after the first stage of computation of positional information.

Motion-direction sensitivity was seen in nuclei with neurons that responded to sound from more than one spatial locus or more than one ITD (lateral lemniscus, ICc-core, ICc-ls) and in nuclei that responded only to stimuli from one spatial locus or one ITD (ICx, OT). The neurons in the former nuclei are narrowly tuned to frequency and are situated at hierarchically lower stations within the sound-localization networks than the latter (Moiseff and Konishi 1983; Knudsen 1984). A convergence of many frequency channels occurs in the projection from the ICc-ls to the ICx (Knudsen and Konishi 1978a; Knudsen 1984; Takahashi and Konishi 1986; Wagner et al. 1987), and this convergence enables the neurons in the ICx and OT to unambigously represent one spatial locus.

Since neurons carrying motion-direction signals converge in ICx, it must be guarantied that the averaging does not distort the motion-direction sensitivity. This requires a very precise spatial convergence. In addition, the temporal jitter in the converging signals may not be too large. Since the neurons express both positional and motion sensitivity, and since the motion-detection step is probably located before the convergence takes place, it is possible to discuss the limitations underlying the convergence found with stationary stimuli. The tuning to ITD increases slightly from the ICc to the ICx (Fujita and Konishi 1991), indicating a very precise spatial convergence. In addition it was found that the convergence occurs also in strong temporal synchronism (Wagner 1991). Neurons in both the ICx and the ICc-ls could sense changes in the ITD lasting well below 1 ms, and for this to work the temporal jitter in the single frequency channels must be very small. It seems then, that the neurons in ICx manage not only to compute in parallel different spatial information (Knudsen and Konishi 1977; Takahashi and Konishi 1986; Wagner et al. 1987), but that they can also keep the information about one (moving) source bound together that is endowed to them by convergence from many different frequency channels.

Neural mechanism of acoustic motion sensitivity

This paper reports some temporal cues of a stimulus that influence the acoustic motion-direction sensitivity. Since spontaneous activity is very low in all these neurons (Wagner 1990), all responses, whether to stationary or to moving sounds, were mainly due to a direction-independent excitation. By comparing the responses of one neuron to stationary and moving sounds, we could show that in many neurons the responses in the null direction were suppressed, i.e. a direction-dependent inhibition (DDI) was present in these neurons. This observation was substantiated by introducing gaps in the stimulus sequence, because 1) gaps often led to a relative increase of the response in the null direction compared to the preferred direction, and 2), after the introduction of gaps, responses could be elicited from more spatial loci. Earlier work demonstrated the existence of inhibition in the auditory system (Knudsen and Konishi 1978b; Carr et al. 1989; Fujita and Konishi 1991). Part of this inhibition is direction-independent (Knudsen and Konishi 1978b). An indication of a

direction-independent inhibition (DII) also came from the observation that the responses to stationary stimuli were often higher than the responses to moving stimuli, because lateral inhibitory interactions may reduce the response in the latter but not in the former stimulus paradigm. Thus, as a third factor, a direction-independent inhibition influenced the responses. An indication of a direction-dependent excitation was seen in only a minority of neurons, and is not considered further.

These observations were combined to a hypothetical, two-stage acoustic motion detector (Fig. 13). While the excitatory responses at the preferred ITD are well established (Fig. 13a), much of the rest of the scheme is speculation. In the first stage, a direction-dependent inhibition is supposed to cause a differentiation in the response between movement in two opposite directions (Fig. 13b). However, motion-direction sensitivity is still low. This first stage might be accomplished at the level of the lateral lemniscus or the ICc. In a second step, a direction-independent inhibition might cause a general reduction in 'neural activity. This would lead to an increase in motion-direction sensitivity (Fig. 13c). There is evidence for this latter step: 1) the lateral inhibition found by Knudsen and Konishi (1978b) in the ICx is direction-independent. Our observation that, in the population, the highest motion-direction sensitivity occurred in the neurons with the lowest response (Fig. 12) is also consistent with the notion of a direction-independent inhibition. The neurons that responded with only a few spikes per stimulus sequence were located in the ICx or OT, i.e. at the highest level of the network. However, it can not be excluded that these two steps occur in parallel in all the nuclei containing motion-direction sensitive cells.

The very general scheme of Fig. 13 has some similarities with the inhibitory scheme of Barlow and Levick (1965). Our first, direction-dependent inhibition resembles some aspects of Barlow and Levick's 'veto' gate (Fig. 1a). The scheme of Fig. 13 shows, however, also similarities with the detector presented in Fig. 1c. For example, the motion-direction sensitivity is computed in two steps. Evidence for a two step visual motion detector has been found in insects (Reichardt 1961; Borst and Egelhaaf 1989) as well as mammals (Levick et al. 1969). Note, however, that such a simple direction-independent inhibition as proposed in Fig. 13, will only work in neurons that do not show much dependence of their response on stimulus variables like stimulus level. Indeed, neurons in the owl's time pathway have a

largely level independent response (Moiseff and Konishi 1981; Sullivan and Konishi 1985). The finding that the motion-direction sensitivity depends on both gap duration and apparent velocity rules out models that contain a constant delay. In most current visual motion detectors the delay is implemented by a low-pass filter (for a review see Borst and Egelhaaf 1989). Simulations are currently being carried out to test whether the responses described here by varying velocity and gap duration can also be explained in this way. Preliminary evidence suggests that this may be possible (Wagner unpublished).

Relevance for behavior

Motion signals in the environment may be caused in two principally different ways. First, if the observer is stationary, the movement of an object may cause the sensation of motion. On the other hand, if the observer moves, the objects in the environment move relative to the observer. We tested for rotational-motion sensitivity in the owl, and found that the neurons were motion-direction sensitive in a broad velocity range. Most conspicuously the range of velocities extends to very high angular velocities that would be generated in head turns (Knudsen et al. 1979; Moiseff 1989; Wagner 1991), but usually not by moving objects. Thus, these neurons are able to sense self-motion of the owl. Since we did not probe the low velocity range it is not clear whether these neurons can also sense object motion.

In conclusion, our study is a first step in elucidating the mechanisms underlying the acoustic-motion sensitivity. With a simple apparent-motion stimulus we could show that some of the mechanisms resemble those also found for visual motion detectors. More experimental and theoretical work is, however, necessary before we can determine whether motion is processed similarly in the auditory and visual systems.

Acknowledgements

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Figure legends

Fig. 1: Schematics of motion detectors. a) inhibitory Barlow-Levick scheme, b) excitatory Barlow-Levick scheme, c) Reichardt-type correlation detector. R: receptor inputs 1 and 2, SS: spatial separation $\Delta\phi$, TA: temporal asymmetry, F: temporal filters, Δt: delay, NL: non-linearity, M: multiplication, 'and': interaction as in a logical 'and' gate; 'and not': interaction as in a logical 'and not' gate; Sum: summation. The function of the scheme shown in a) is explained in the text.

Fig. 2. Test apparatus (a) and stimulus structure (b). a) Seven free-field speakers were placed in front of the owl at a distance of 100 cm. Apparent motion was generated by activating the speakers in sequence, either in a counter-clockwise (CCW, from 1 to 7) or in a clockwise direction (CW, from 7 to 1). b) The moving stimulus is characterized by the duration of the sound from individual speakers ('duration') and the time lapsed between activation of successive speakers (ISI). If these times differ, a silent interval ('gap') or a stimulus overlap may occur.

Fig. 3. Basic tests for motion-direction sensitivity. Three basic tests were performed to test a neuron's motion-direction sensitivity. First the neuron was stimulated with condition 1 (a), then with condition 2 (b), and finally with condition 3 (c). The response is shown as a raster in which each dot represents the arrival of a spike, and as histograms that represent the summed activity. The bin width was equal to the ISI. The neuron depicted showed a high motion-direction sensitivity when stimulated with condition 1 or condition 2. No directional bias was observed with the one-speaker test. The ISI was 95 ms and stimulus duration was 100 ms. The motion-direction is indicated by the step functions above the histograms. Rising steps represent motion in the CCW direction, i.e. from speaker #1 to speaker #7, while falling steps represent stimulus motion in the CW direction, i.e. from speaker #7 to speaker #1. The step length indicates the stimulus duration at each speaker.

Fig. 4: Example of a neuron without motion-direction sensitivity. In this cell the same basic tests applied to the cell shown in Fig. 3 were performed, and the same conventions and symbols were used. Note the symmetrical histograms in a) and b), which indicate an insensitivity to motion-direction. The one-speaker test (c, condition 3), also produced a symmetrical response.

Fig. 5 Sampling of motion-direction sensitivity. In the examples were depicted different apparent velocities (ISI 240 ms: a, b; ISI 95 ms: c-f), and different preferred directions (CCW: a, b, d, e; CW: c, f), and responses obtained from different nuclei: (lateral lemniscal nucleus VLVp): a, ICc-core: e, ICc-ls: c, ICx: f, OT: d), and examples for high (c-e), middle (b, f) and low (a) motion-directions sensitivities are shown. Note that the location of recording in (b) could not be determined positively. Symbols are as in Fig. 3.

Fig. 6. *Velocity independence of motion-direction sensitivity.* This neuron was tested with three different apparent velocities (a: 125 deg/s, b: 310 deg/s, c): 1200 deg/s). Gap duration was -5 ms in all cases. The response with all tested velocities showed the same high motion-direction sensitivity, indicating that the motion-direction sensitivity was largely velocity independent. Note the different time scales on the x-axis.

Fig. 7. Introduction of a gap decreased motion-direction sensitivity. The decrease of the motion-direction sensitivity may be judged by comparison with responses in the earlier figures as indicated below: a) ISI 95 ms, gap 71 ms, same neuron as shown in Fig. 5e; b) ISI 95 ms, gap 60 ms, same neuron as shown in Fig. 3; c) ISI 240, gap 205 ms, same neuron as shown in Fig. 5b; d) ISI 240, gap 205 ms, same neuron as shown in Fig. 6. Note that after introduction of a gap a response could be elicited from more speakers, and this was the main reason for the change in the DI.

Fig. 8. Response as a function of gap duration. The change of the number of spikes (recorded in 10 stimulus repetitions) with gap duration is shown for different conditions and

different types of responses. The number of spikes in the null direction is indicated by the triangles, and the number of spikes in the preferred direction is indicated by the circles. Note that the decrease of motion-direction sensitivity with gap duration, which can be inferred from the convergence of the regression lines at the right side of the plots, may result from increasing spike numbers in the null direction (a), decreasing spike numbers in both directions (c), decreasing spike numbers in the preferred direction (b), or decreasing spike numbers in the preferred direction combined with an increase in the spike numbers in the null direction (d).

Fig. 9. Influence of gap duration on the signed DI. The introduction of a gap in the stimulus sequence decreased the signed DI for neurons preferring the CCW direction (a-c) and increased the signed DI for neurons with a preferring the CW direction (d). This effect was independent of the apparent velocity (ISI 95 ms: a, c ; ISI 240 ms: b, d). The dependence of the signed DI on gap duration was linear and could be characterized by the slope of the regression line.

Fig. 10. Dependence of the signed DI on gap duration at different velocities. The slopes of the regression lines of the dependence of the signed DI on gap duration differed for different ISIs (a, b; circle: 95 ms ISI, triangle: 240 ms ISI). If the signed DI was plotted as a function of the duty cycle (see text), the slopes calculated from the dependence on either ISI were similar (c, d), indicating that the apparent velocity was important for the mechanism underlying the motion-direction sensitivity, and that the duty cycle was the important response variable.

Fig. 11. Distribution of the slopes obtained from the regression between the DI and gap duration. For a comparison of different cells the signed DIs for the individual gap durations were first normalized with respect to the signed DI measured with -5 ms gap duration and 95 ISI. The slopes were calculated from these normalized, signed DIs. In a second step, the sign of the slopes of the cells that have a CW preferred direction was changed so that the slopes of all cells became comparable. The sample is based on 23 neurons (95 ms ISI, circles)

and 20 neurons (240 ms ISI, triangles). a) the slope calculated from the regression of the normalized DIs on gap duration. Note the different means of the slopes. b) The slopes calculated from the regression of the signed DIs on the duty cycle were not different.

Fig. 12. *Motion-direction sensitivity and neural activity.* The absolute value of the DI is plotted as a function of the number of spikes recorded in 10 stimulus repetitions for all neurons that proved to be motion-direction sensitive by a χ^2-test. The sample comprises 61 neurons from all nuclei. Note the decrease of motion-direction sensitivity with increasing neural activity.

Fig. 13. Working scheme that explains the data. a) The ITD-curve of a neuron, i.e. the response of a neuron to stationary sound, indicates that this curve is shaped mainly by an excitation at the preferred ITD, and less so by an inhibition at the non-preferred ITDs. Note spontaneous level (dashed line). b) Motion-direction dependent inhibition (DDI) in the null direction leads to a low directionality index (DI=0.3). c) If, in a second stage, a direction-independent inhibition (DII) is added (see also b), the direction sensitivity increases (DI=.75). Note that the presence of a direction-independent inhibition may explain the curve of Fig. 12.

Fig 1
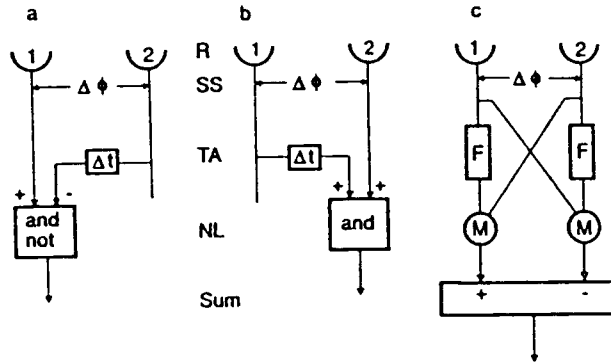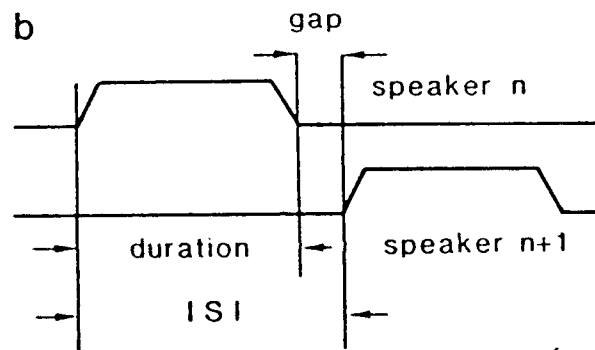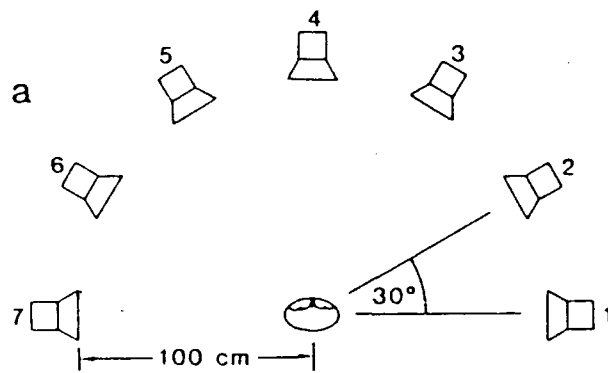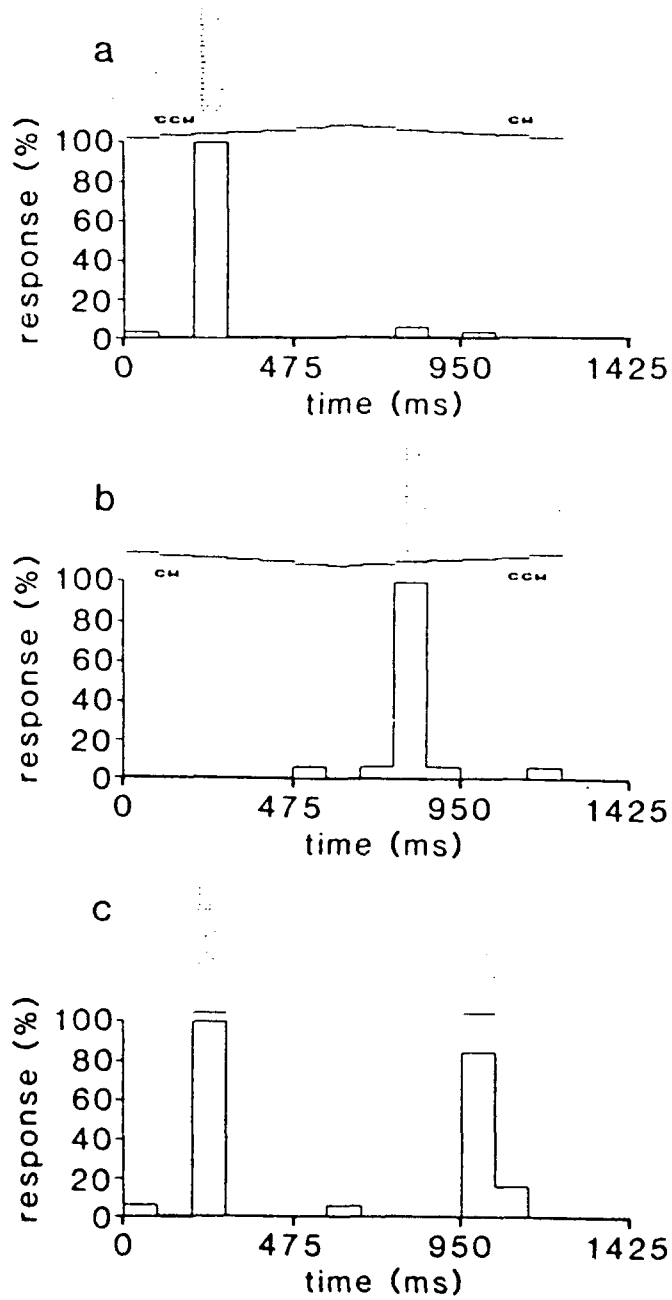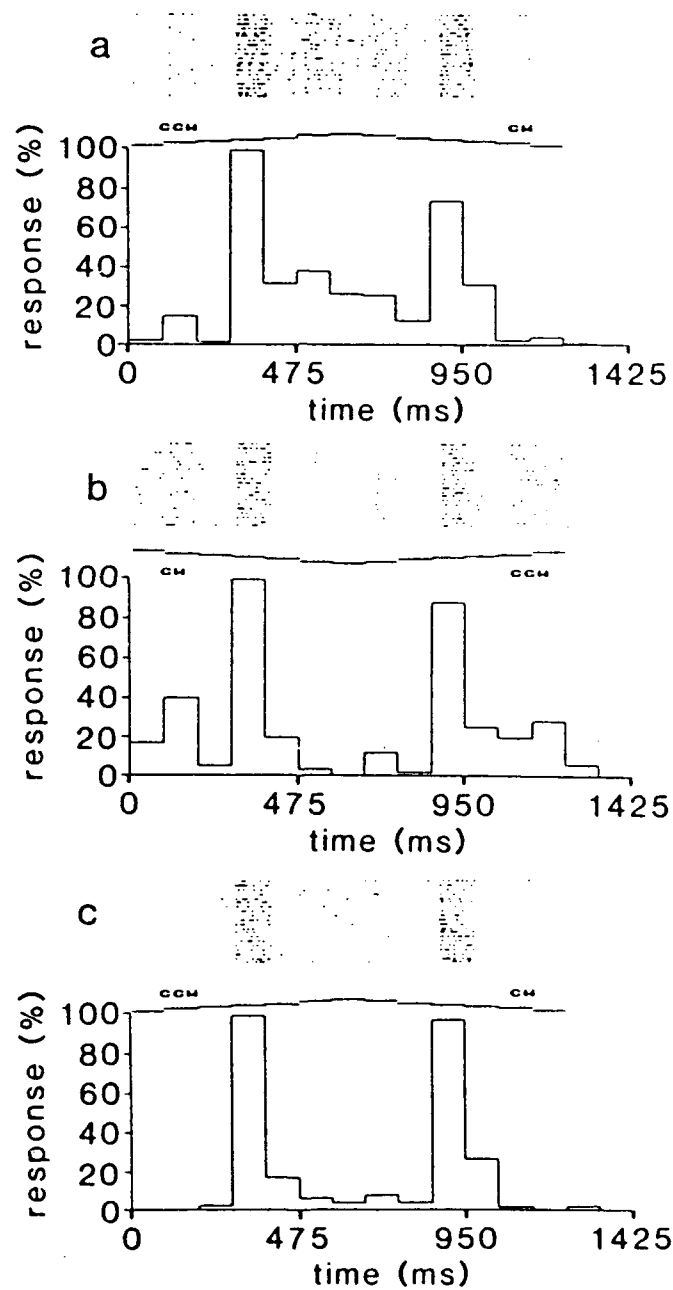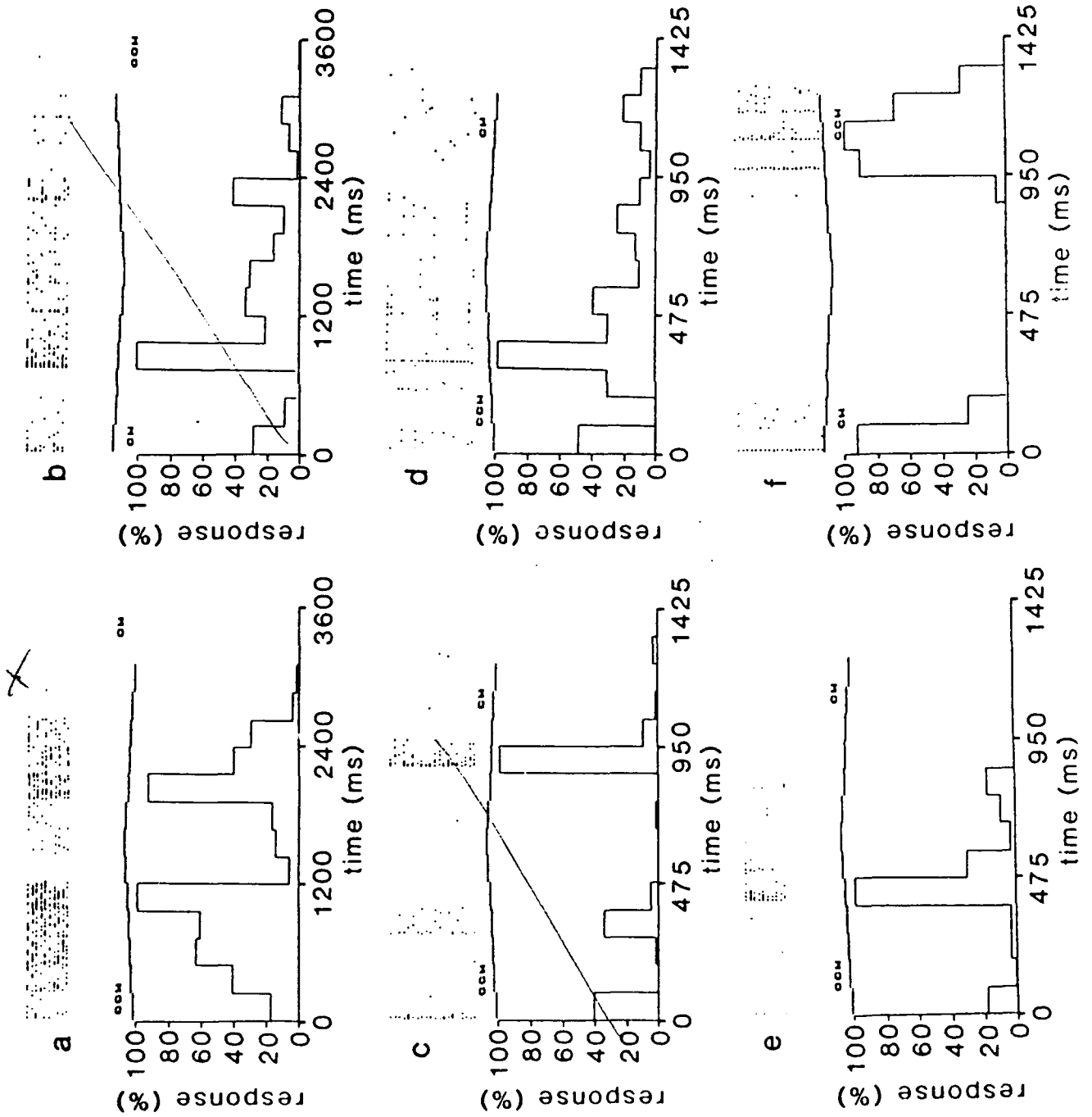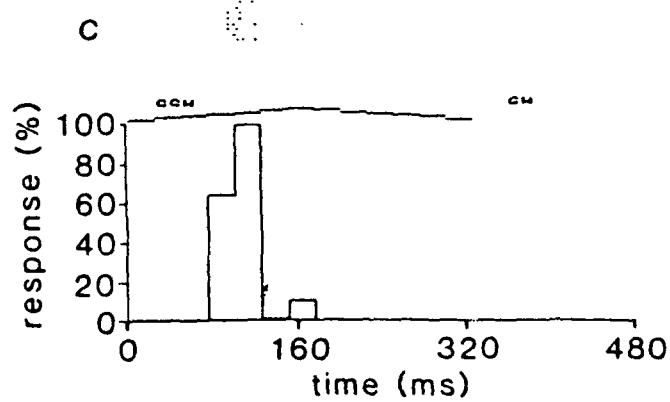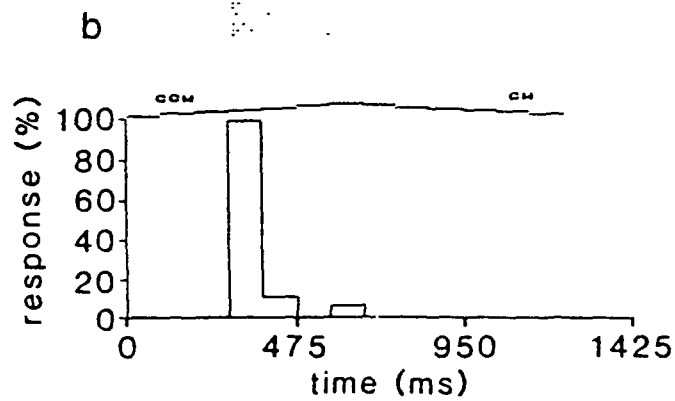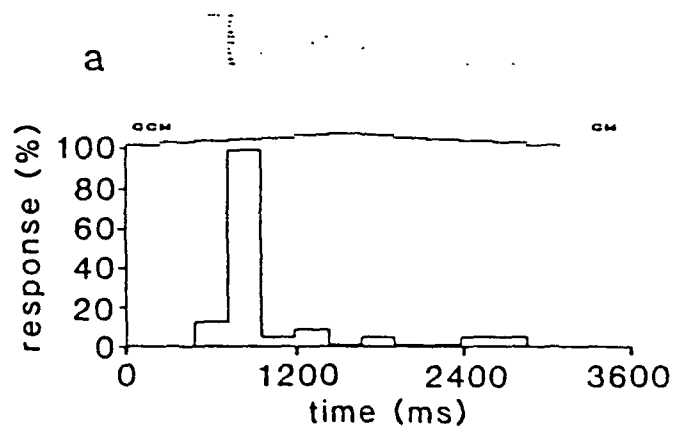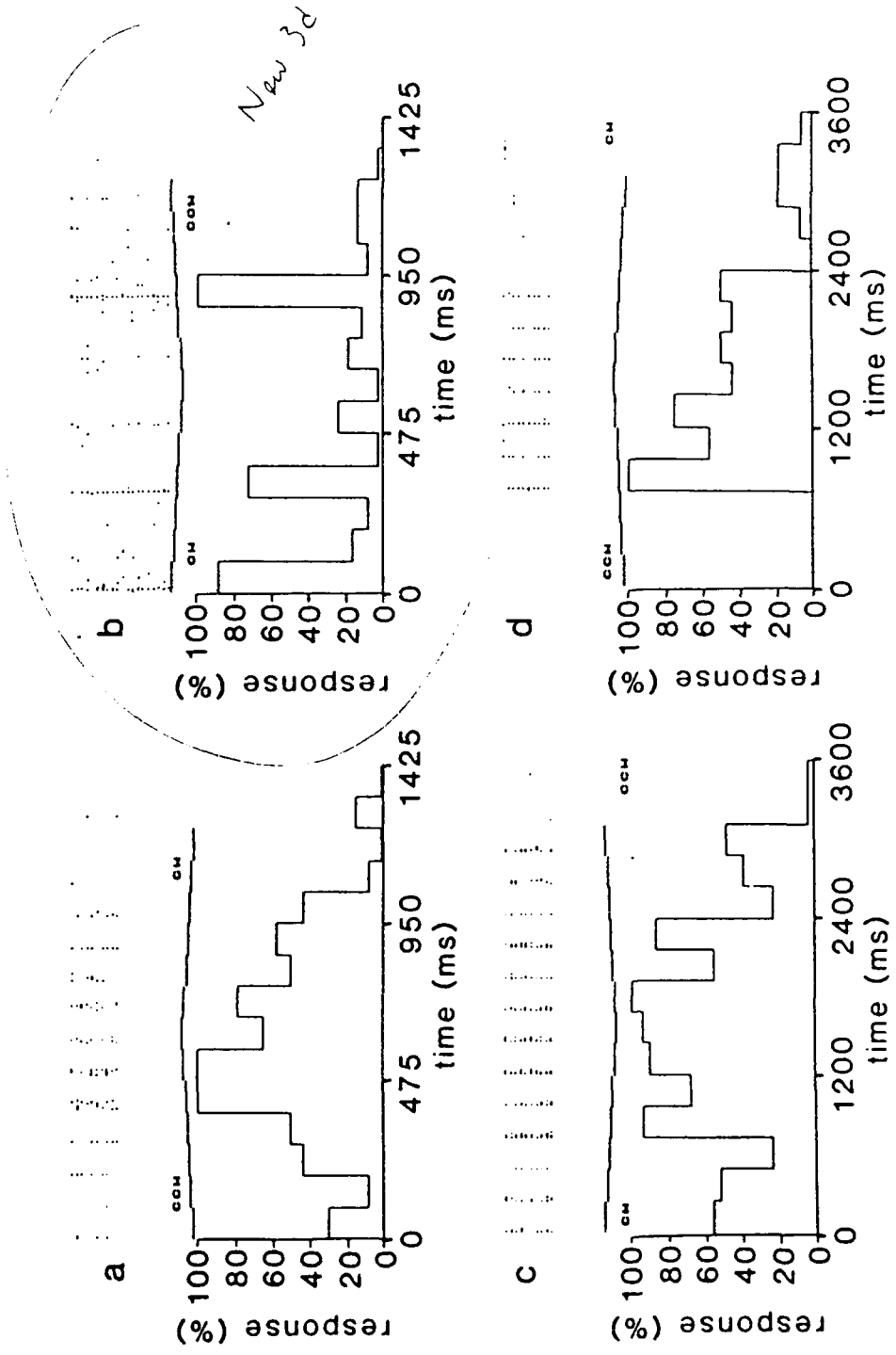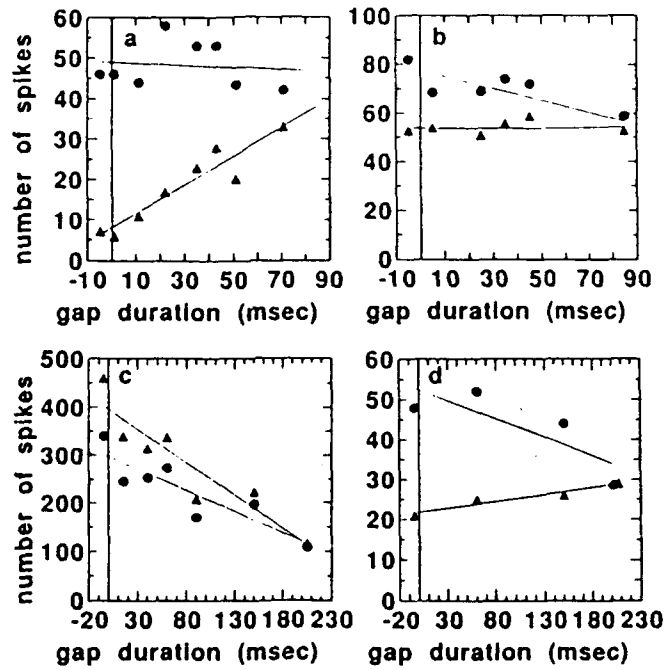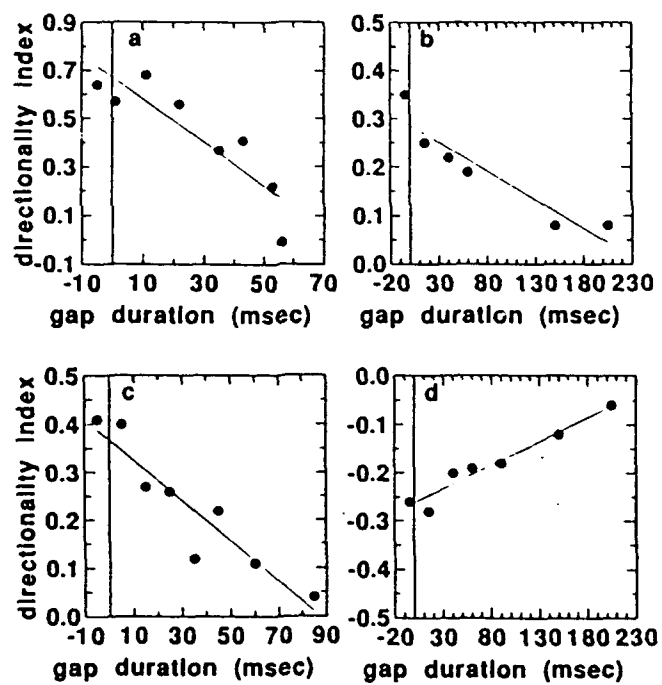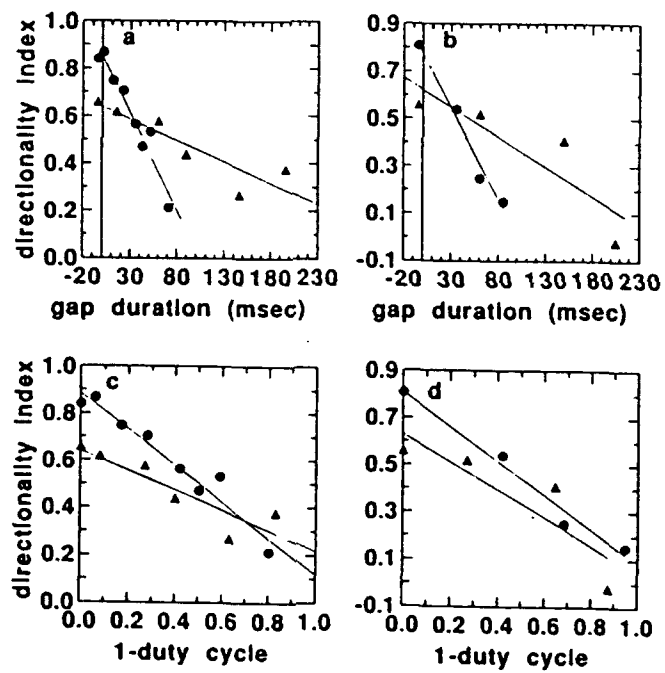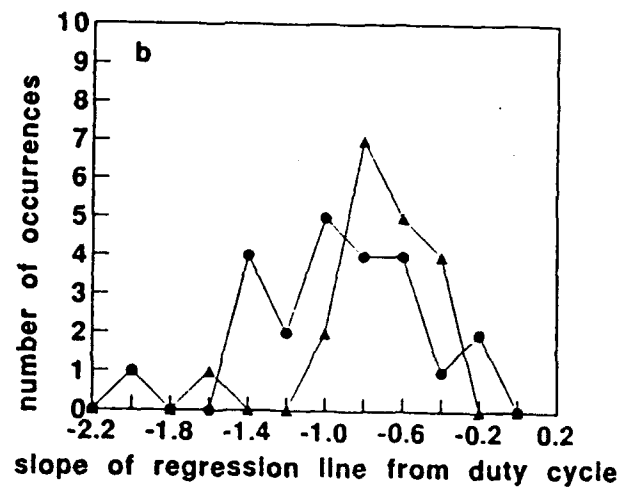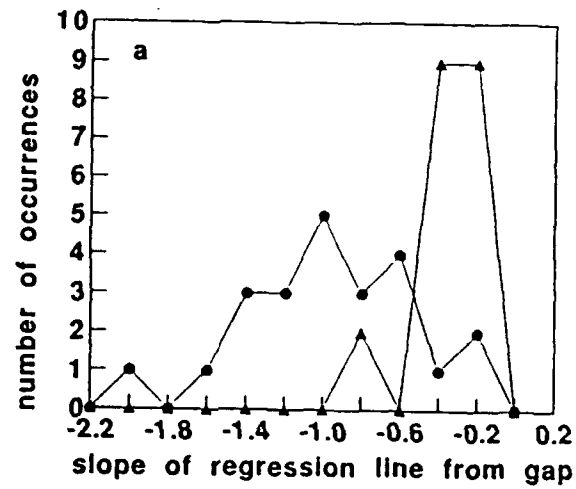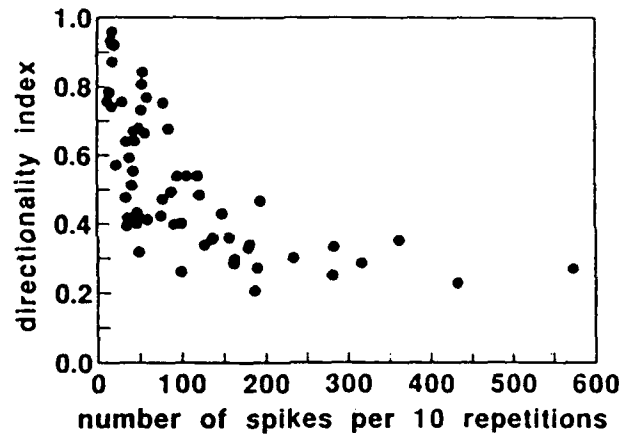
R		
SS		
TA		
NL		
Sum		

Fig 2

a

4

5

3

6

2

30°

7

1

|— 100 cm —|

b

gap

speaker n

duration

speaker n+1

I S I

Fig 3

a

b

c

Fig 4

a

b

c

110

Fig 5

lii

Fig 6

a

b

c

Fig 7

New 3d

b

d

a

c

113

Fig 8

Fig 5

Fig 10

116

slope of regression line from gap

slope of regression line from duty cycle

Fig 12

number of spikes per 10 repetitions

118

Neuroethology

AA

Complete the following if no address appears in the box.
If there are errors, make corrections below. Please type or print clearly.

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MOTION UNMASKING OF AUDITORY TARGETS

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In nature, sound-sources move and signals are accompanied by background noise. Noting that motion helps the perception of visual stimuli, we tested whether motion similarly facilitates the detection of acoustic targets, at the neuronal level. Auditory neurons in the central nucleus of the barn owl's inferior colliculus (ICc), due to their selectivity for interaural phase difference ($\Delta\Phi$), are sharply tuned to the azimuth of sound-sources and are arrayed to form a topographic map of $\Delta\Phi$. While recording from single ICc neurons, we presented tones that simulated either moving or stationary sound sources with or without background noise.

We simulated a moving source by presenting tones of slightly differing frequencies to each ear. Under this condition the sounds start out in-phase binaurally, but over time, the phase angle in the ear receiving the higher frequency advances relative to that in the opposite ear, until they are once again in-phase. This simulates a source moving in an arc toward the higher-frequency ear with an angular speed proportional to both the interaural frequency difference and the period of the stimulus tone, which, in our tests, was at each cell's best frequency. This stimulus is also known as "binaural beats". Stationary signals consisted of 1-sec tones of identical frequencies presented to the left and right ears at fixed $\Delta\Phi$ values. Stationary tonal stimuli were also amplitude-modulated for some tests by multiplying the carrier frequency by a triangular envelope. The envelopes were binaurally in-phase, had frequencies equal to the ΔF used in that cell's binaural beats test, and modulated the tones to a depth of 75%. Each type of signal was masked by binaurally-uncorrelated, broadband noise. The $\Delta\Phi$-sensitivity of the ICc neurons under the various conditions was quantified by plotting spike-rate as a function of $\Delta\Phi$ and computing a measure analogous to the standard deviation of the distribution, called the vector strength. We studied only those ICc cells (N = 59 cells in 6 birds) that showed a significant sensitivity ($p < 0.01$) for $\Delta\Phi$ as judged by a statistical test of the vector strength (Rayleigh test; Durand and Greenwood, 1958 *J. Geol.* 66:229-238.).

Our findings suggest that neurons of the ICc are capable of exploiting the motion of sound sources. Tones that mimicked a stationary source could be obscured by noise, as judged by a neuron's vector strength, but if the $\Delta\Phi$ changed continuously thus mimicking motion, the neuron's $\Delta\Phi$ specific response re-emerged. The latter could not be observed when the stimulus mimicked a stationary, amplitude-modulated tone-source, suggesting that a change of position was required rather than a simple time-varying stimulus. The cells also showed a higher selectivity for $\Delta\Phi$ in the absence of noise if $\Delta\Phi$ changed continuously over time than when a succession of fixed $\Delta\Phi$ values was presented, suggesting that the place-code for space in the ICc is of finer grain for moving sources ($p < 0.0001$, Wilcoxon paired signed-ranks test).

As the phenomena described above were demonstrated with tonal stimuli, they can be subserved by neuronal interactions within a single isofrequency layer of the ICc. Furthermore, since binaural beats, but not amplitude modulations, produce these phenomena, it is likely that the mechanism itself involves interactions between cells that represent adjacent $\Delta\Phi$ values.

SIMULATED MOTION ENHANCES NEURONAL SELECTIVITY
FOR A SOUND LOCALIZATION CUE IN BACKGROUND NOISE

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Abstract

In nature, sound-sources move and signals are accompanied by background noise. Noting that motion helps the perception of visual stimuli, we tested whether motion similarly facilitates the detection of acoustic targets, at the neuronal level. Auditory neurons in the central nucleus of the barn owl's inferior colliculus (ICc), due to their selectivity for interaural phase difference ($\Delta\Phi$), are sharply tuned to the azimuth of sound-sources and are arrayed to form a topographic map of $\Delta\Phi$. While recording from single ICc neurons, we presented tones that simulated either moving or stationary sound sources with and without background noise.

We found that the tuning of cells in the ICc for $\Delta\Phi$ was sharper for stimuli that simulated motion than for those that simulated stationary targets. The neurons signaled the presence of a tone obscured by noise better if the tone moved than if the tone remained stationary. The resistance to noise observed with moving stimuli could not be reproduced with the temporal modulation of the stimulus amplitude, suggesting that a change of position over time was required.

Motion plays an important role in visual perception. As early as 1878, it was demonstrated that shadows that were too dim to detect when stationary, became visible when moved, suggesting that motion aids the detection of visual stimuli (Schneider, 1878 -- as cited in Boring, 1948). More recently, studies have shown that movement or flicker of a pattern is detectable at contrasts that are too low for identification of the pattern (Kulikowski and Tolhurst, 1973). Other studies have demonstrated that motion is critical for the extraction of figure from ground, the most notable demonstration being the random-dot kinematogram in which the coherent motion of a subset of randomly positioned dots causes the outlines of an object to stand out from the background (Anstis 1970, Braddick 1974).

Does the motion of sound sources similarly facilitate their detection? In man, who is relatively insensitive to acoustic motion (Grantham, 1986), the motion of a sound source does not facilitate its detection (Wilcott and Gales, 1954; Robinson, 1971; Grantham and Luethke, 1988). By contrast, certain echolocating bats are better able to avoid obstacles and detect targets amidst clutter if the objects move (Simmons, 1981; McCarty and Jen, 1983).

The barn owl (*Tyto alba*), although lacking the bat's ability to echolocate, is nevertheless a keen auditory predator capable of striking moving prey in absolute darkness (Payne, 1971). Its brain has considerable specializations for such purposes. Most remarkably, auditory neurons in its inferior colliculus have discrete spatial receptive-fields and are systematically arrayed to form a topographic map of space (Knudsen and Konishi, 1978; Wagner et al., 1987). Some of these neurons, moreover, are sensitive to the direction of stimulus motion along the horizon (Wagner and Takahashi, 1990). Thus, despite the negative findings in man, we expected the owl's auditory system to exhibit adaptations for the exploitation of acoustic motion.

In the present study, we recorded from single auditory neurons in the central

nucleus of the barn owl's inferior colliculus (ICc) that are responsive to tonal stimuli and are selective for interaural phase difference ($\Delta\Phi$), the binaural cue correlated with stimulus azimuth (Knudsen and Konishi, 1979; Moiseff and Konishi, 1981a). Within the ICc, these neurons form a topographic map of the horizontal meridian (Wagner et al., 1987). The response of neurons in the ICc to stimuli that simulated tones from moving or stationary targets were compared under noisy and quiet background conditions.

We simulated a moving source by presenting tones of slightly differing frequencies to each ear. Under these conditions, $\Delta\Phi$ changes smoothly over time, as would a tone from a source moving in an arc along the horizon, at ~ constant angular speed. In man, this stimulus paradigm is known to produce an illusion of motion, and the perception is termed "binaural beats." The analogous psychophysical studies have not been done in owls. However, since the stimulus configuration generates smooth changes in $\Delta\Phi$ and owls use $\Delta\Phi$ as the cue for the horizontal location of the source, we will use the terms binaural beats, moving tones, and motion, interchangeably.

Materials and Methods

Surgery and Animal Care

All procedures were carried out under a protocol approved by the Institutional Animal Care and Use Committee of the University of Oregon. Adult barn owls (*Tyto alba*, N = 6) were anesthetized by intramuscular injections of ketamine (0.1 ml/hr; Vetalar 100 mg/ml, Parke-Davis) and diazepam (0.05 ml/hr; Diazepam C-IV 5 mg/ml, LyphoMed) and given a prophylactic dosage of ampicillin (0.2 ml intramuscular; Polyflex, 250 mg/ml Aveco). The owl was placed into a stereotaxic device that held its head tilted downwardly at a 45° angle. The scalp was infused with a local anesthetic (2% lidocaine HCl, Xylocaine, Astra Pharmaceuticals) and incised, and a stainless steel plate was cemented to the rostral portion of the cranium. After the plate was firmly attached,

the earbars that held the head in position were replaced with miniature earphones. A hole about 0.7 cm^2 was opened in the skull with sterile rongeurs. Heavy mineral oil (Spectrum Chemical) was applied to the dural surface to prevent desiccation. Body temperature was monitored and was maintained with a circulating-water heating pad. Fluid levels were maintained by periodic subcutaneous injections of 5% dextrose in lactated Ringer's solution (Abbot Labs).

As we were attempting to document a new phenomenon, we surveyed the ICc of each bird extensively. In order to minimize the stress on the bird, we ran two, 15 to 20-hour sessions separated by a 4 to 7-day recovery period, instead of a single lengthy procedure. At the end of the first session, the craniotomy was closed with dental cement (Vitrabond, 3M Inc.) and the scalp was sutured and covered with a topical antibacterial cream (Bacitracin-Neomycin-Polymyxin Ointment, E. Fougerra & Co.). Before returning the bird to a recovery cage, it was given 0.2 cc of dexamethasone and 0.2 cc of vitamin B complex intramuscularly and 10 to 20 cc of 5% dextrose in lactated Ringer's solution intravenously. The recovery cage was maintained at 34° C, 25% humidity, and 30% O$_2$. The bird's activity was monitored hourly until it fully recovered.

Birds were euthanized at the end of the second session by an overdose of pentobarbital (Nembutal, Abbot Laboratories) and were exsanguinated (0.9% NaCl) and fixed (3.75% paraformaldehyde in 0.1M phosphate buffer, 7.4 pH) transcardially. The brains were removed and processed for histology to confirm the locations of the electrode penetrations.

Electrode locations relative to the cytoarchitectural boundaries of the inferior colliculus were confirmed by histological examination to be within the ICc (see Takahashi, et al., 1987 and Takahashi and Konishi, 1988a,b for descriptions of the inferior colliculus and surrounding structures).

Stimulus Generation and Data Analysis

Tonal stimuli were produced by a dual-channel synthesizer (Hewlett Packard 3245A Universal Source). The analog signals were scaled down with programmable attenuators (Modular Instruments Inc.) to achieve average binaural levels that were 20-30 dB *above* neuronal threshold. The attenuated signals were amplified with a stereophonic amplifier (McIntosh 754) and transduced with miniature ear phones matched in amplitude and phase (Sony MDR-E272).

In order to produce tones with continuously varying $\Delta\Phi$, sine waves with slightly differing frequencies were presented to the left and right ears (Kuwada et al., 1979; Moiseff and Konishi, 1981a; Yin and Kuwada 1983; Moiseff and Haresign, in press). The sounds start out in-phase binaurally, but over time, the phase angle in the ear receiving the higher frequency advances relative to that in the opposite ear, until they are once again in-phase. This simulates a source moving in an arc toward the higher-frequency ear with an angular speed proportional to the absolute value of the interaural frequency difference (ΔF) and the period of the stimulus tone (τ), which, in our tests, was at a cell's best frequency:

$$\text{Angular Speed } = |\Delta F| \tau / k \qquad\qquad \text{Eqn. 1}$$

The term, k, is a constant relating interaural time difference (ITD) to azimuth and has been computed to be 2.3 μsecs of ITD per degree of azimuth for the adult barn owl (Moiseff, 1989). A graphic representation of binaural beats is shown in a report by Kuwada and colleagues (1979) (also Yin and Kuwada, 1983).

All cells of our sample (N = 59 in 6 birds) were tested with stimuli simulating rightward and leftward motion. All but 10 of the cells were tested with ΔFs of 1, 2, or 4 Hz. Using Equation 1, the angular speeds simulated for these neurons ranged from 52

degrees of azimuth per second (ΔF = 1 Hz; τ = 120 μsec) to 278 degrees of azimuth

per second (ΔF = 4 Hz; τ = 160 μsec). This is within the range of angular speeds

encountered by the owl during flight or the movement of prey. Of the 10 remaining

cells, 1 was tested at 6 Hz, 8 at 8 Hz, and 1 at 16 Hz, resulting in angular speeds of up

to 1360 degrees of azimuth per second (ΔF = 8 Hz; τ = 391 μsec).

Moving tones lasted for 11.5 sec, during which time we recorded spikes. Spikes

occurring during the first 1.5 beat cycles and after the offset of the stimulus were

discarded in order to avoid neuronal responses to stimulus onset and offset. The spike

times were binned with respect to the period of the binaural beat so as to plot the

number of spikes as a function of $\Delta\Phi$ at a resolution of 1/41th of a cycle. The vector

strength, a measure of tuning to $\Delta\Phi$, was computed from these histograms (Goldberg

and Brown, 1969; Kuwada and Yin, 1983). A vector strength of 1 indicates that all

spikes are in one bin, and a vector strength of 0 indicates that all spikes are evenly

distributed throughout all bins. We interpreted the vector strength as the degree to

which a cell can detect and signal the presence of a stimulus.

Stationary signals consisted of 1-sec tone bursts of identical frequencies presented

to the left and right ears. The $\Delta\Phi$ remained fixed for the duration of a burst and was

incremented between bursts in 41 steps from +0.5 to -0.5 cycles. The number of spikes

for each tone burst were plotted as a function of $\Delta\Phi$, and the resulting histogram was

analyzed as described above for binaural beats. Spikes occurring during the first 20

msecs and after the end of each tone burst were discarded to avoid onset and offset

responses.

Stationary tonal stimuli were also amplitude-modulated for some tests. In these

cases, the tones at each $\Delta\Phi$ were multiplied by a triangular envelope from a digital to

analog converter (Modular Instruments Inc.). The envelopes were binaurally in-phase, had

frequencies equal to the ΔF used in that cell's binaural beats test, and modulated the

tones to a depth of 75%. Histograms of spike counts versus $\Delta\Phi$ for these amplitude modulated tones were then compiled and analyzed as discussed above.

Signals were embedded in noise by summing the analog output of the signal generators of the left and right sides with broad band noise having a flat spectrum (after transduction) between 1 and 10 kHz. The noises to the ears were taken from two, independent, random-noise generators and were therefore binaurally uncorrelated. The signal-to-noise ratio (S/N) was computed as the quotient of the root-mean-square energy in the signal band to that in the noise from 1 to 10 kHz. The total energy was kept constant for the different S/Ns tested.

The responses of our neurons under various test conditions were compared using the Wilcoxon paired signed-ranks test (Sokal and Rohlf, 1981) except where noted otherwise.

Results

General Properties of ICc Cells

A typical electrode pass through the barn owl's inferior colliculus began with multi-unit responses to dichotic stimuli, that gave way to responses from isolated cells selective for frequencies of about 2 kHz. More deeply, the best frequencies increased to a maximum of about 9 kHz, as expected from earlier descriptions of tonotopy in the ICc (Knudsen and Konishi, 1978; Wagner et al., 1987). The single units we encountered were generally excitable through either ear, with the contralateral ear usually providing a stronger input. The cells of the ICc could be distinguished from those of its lateral neighbor, the external inferior collicular nucleus, by their stronger response to tonal stimuli, their higher selectivity for frequency, and by their relative insensitivity to interaural level difference. Although we isolated numerous cells in the course of an electrode pass, we studied only those ICc cells (n = 59 cells in 6 birds) that showed a

significant selectivity for Δφ as judged by a statistical test of the vector strength (Rayleigh test with p < 0.01; Durand and Greenwood, 1958). When binaural beat stimuli were presented, the neurons typically discharged spike-bursts that were locked to the period of the binaural beat, and thus occurred at approximately the same Δφ within each binaural beat cycle. This beat-locked spiking continued throughout the course of the stimulation without any evidence of fatigue. The spiking of neurons in the ICc was not phase-locked to the carrier frequency presented to either ear.

Our sample of cells had best frequencies between 2 and 8.3 KHz with 54 of 59 cells having best frequencies above 4 KHz. It is not surprising that such high-frequency cells would respond to Δφ in the barn owl, whose 8th nerve and cochlear nucleus phase-lock up to 9 KHz (Sullivan and Konishi, 1984). The use of these high frequencies excludes the involvement of the interaural canal, which connects the left and right middle ears of birds and can transmit sounds between the ears. In the barn owl, frequencies above 4 KHz are severely attenuated within the canal and neuronal responses to these frequencies are not affected by crosstalk (Moiseff and Konishi, 1981b). Additionally, the 5 cells of our sample tested with frequencies at or below 4 KHz showed no qualitative differences from cells tested with higher frequencies in response to motion or stationary stimuli.

Responses to Tones in a Quiet Background

Cells were generally more selective for Δφ when presented with moving stimuli than with stationary stimuli. Figure 1 shows histograms of spike rates as a function of Δφ, obtained with stationary tones (left column), and with simulated leftward (center column), and rightward motion (right column) for four representative cells. Each stationary histogram is normalized to its own maximum and the motion histograms are normalized to either the leftward or rightward maximum, whichever was higher.

Comparison of absolute spike-rates obtained with stationary and moving stimuli is not possible without making certain assumptions (see Discussion).

All of the histograms shown in Figure 1 are peaked, indicating that the neurons have a preferred ΔΦ regardless of whether or not the stimulus simulates motion. The shapes of the histograms are similar to those depicted in reports by others (Kuwada et al., 1979; Yin and Kuwada, 1983; Reale and Brugge, 1990; Spitzer and Semple, 1991; Moiseff and Haresign, in press). For our sample as a whole, however, vector strengths obtained with leftward or rightward motion were greater than those obtained under stationary conditions ($p < 0.0001$, N = 52 and N = 50 for leftward and rightward pairs, respectively). The cells of Figures 1A and B demonstrate most clearly that with moving tones, the skirts of the histogram relative to the peak are lower in the motion condition than in the stationary condition. In fact, in Figure 1B, one can see that motion completely silences responses between +0.35 and +0.5 cycles which were effective when the stimulus was stationary. ΔΦ histograms are thus narrower and vector strengths (r) higher for the motion condition. Figure 1C shows results from a third cell for which the vector strengths obtained with motion were higher than those obtained with stationary stimuli, but less dramatically so. Only two cells, one of which is depicted in Figure 1D, showed a higher vector strength for stationary conditions than for motion, and in neither cell was the difference as dramatic as in Figures 1A and B.

The observation that motion will completely silence a cell at non-optimal ΔΦ values, suggests that inhibition is at least one mechanism by which motion enhances ΔΦ sensitivity beyond levels seen with stationary stimuli. The weakness of stationary vector strengths relative to motion vector strengths, however, might also be due to fatigue. A stationary stimulus left at preferred ΔΦ values for 1 sec might fatigue the cell, whereas at less effective ΔΦ values, where firing would be weaker, the cell would not fatigue. A cell's response would therefore be constrained only at the stronger stationary ΔΦ values.

In such a case, vector strengths should diminish with time from the onset of a stimulus. To examine this possibility, we divided the response to the 1-sec stationary tone at each bin into 250-millisecond quartiles. Vector strengths obtained with moving tones were then compared to vector strengths for stationary stimuli computed from each quartile of the stationary responses. Once again, for our sample as a whole, vector strengths obtained with motion were higher than those obtained from any quartile of the stationary responses ($p < 0.05$). Furthermore, no significant differences were found among vector strengths computed from different quartiles.

Our sample of cells showed little directional preference. Upon comparing the total spike numbers obtained with leftward and rightward motion, we found that only 5 of 45 cells discharged preferentially for one direction at a statistically significant level ($p < 0.05$, χ^2-test). This proportion of directionally selective cells is comparable to that found in the ICc of the cat (Yin and Kuwada, 1983), but less than that found in the subdivisions of the owl's inferior colliculus and optic tectum combined (Wagner and Takahashi, 1990)

Responses to Tones in Noise

We asked how the cells' ability to detect a tonal stimulus is affected by noise. For these tests, moving and stationary tones were combined with interaurally uncorrelated noise, and the response of the neurons was measured over a range of signal to noise ratios (S/N). Interaurally uncorrelated noise, which produces a variety of $\Delta\Phi$ values randomly over time, can be thought of as the auditory analogue of "snow" on a video screen. A neuron's preferred $\Delta\Phi$ and frequency can arise at random, and the neuron's spontaneous discharge therefore tends to increase when interaurally uncorrelated noise is presented alone. A neuron's vector strength was used as an index of its ability to detect a tone. If a neuron is unable to detect the tone, its firing will be

random with respect to the period of the tone, and its vector strength will be zero.

A neuron's ΔΦ-specific response and therefore its ability to report the presence of the target within its receptive field was obscured by background noise. Figure 2 shows ΔΦ histograms at various S/Ns (A-E) for one cell. At each ratio, the histogram on the left was obtained with a stationary stimulus while that on the right was obtained with rightward motion. Each histogram is normalized to the maximal spike rate in its column. The leftward response was indistinguishable from the rightward response and is not shown. At high S/N (S/N = 10, Fig 2A), the neuron displayed the typical selectivity for ΔΦ already described, whether or not the stimulus simulated motion. When noise was added, there was a disproportionate increase in firing at formerly ineffective ΔΦ values, as well as an increased overall activity. In effect, noise broadened the histograms, obscuring the peak (Figs. 2B-E). The vector strengths correspondingly diminished.

Motion of the stimulus allowed the cell to maintain its ΔΦ-specificity. Figures 2C and D show that the peak of the motion histogram (right), relative to the skirts, remained distinct at S/Ns that flattened the stationary histograms (left). The initial rate of recovery from the obscuring effect of the noise was higher for moving stimuli than for stationary stimuli, a point best seen in Figure 3A, which plots vector strength as a function of the S/N for the cell of Figure 2. Figures 3B and C show similar plots for two other cells. In each graph except Figure 3D, the slope of the curve at the lower S/Ns is higher for the motion conditions (triangles) than for the stationary condition (solid circles). In the cell of Figure 3B, the vector strength is higher for motion at the highest S/N tested, whereas in the cells of Figures 3A and C, the vector strength for motion and stationary conditions are roughly equal at the high S/N. Figure 3D shows one of two cases in which the responses to stationary and motion stimuli recovered in the same manner.

Figures 4A and B summarize the differences in vector strengths obtained with moving and stationary stimuli for our sample. Each scatter-plot graphs as a function of

S/N, the difference between motion and stationary vector strengths (r_{mot} and r_{stat} respectively) normalized to the sum of the two vector strengths:

$$\text{normalized difference} = (r_{mot} - r_{stat}) / (r_{mot} + r_{stat}) \qquad \text{Eqn. 2}$$

Positive values indicate that moving stimuli had higher vector strengths and were therefore more detectable to the cell, and negative values indicate that stationary stimuli were more detectable. Figure 4A is for leftward motion and Figure 4B is for rightward motion. These scatterplots show that over a wide range of S/N, there is a strong tendency for moving stimuli to produce higher vector strengths than stationary stimuli in the presence of noise.

Responses to Amplitude-Modulation (AM)

The results above suggest that ICc neurons are better able to signal the presence of stimuli in which a change of position over time is simulated. It is also possible, however, that the results are due to the periodic stimulation of a cell by a stimulus that repeatedly traverses its receptive field, and that a change in the position of the target is not necessary. To test for this possibility, we amplitude-modulated the stimulus synchronously in the two ears, thereby producing a time-varying stimulus without simulating changes in the stimulus's position. Such stimuli would be analogous to a stationary speaker periodically emitting tone-bursts or to a flashing stationary light.

We compared the $\Delta\Phi$ sensitivity of 21 ICc cells to stationary AM tones, stationary unmodulated tones, and moving tones. The stimulus amplitude was modulated by a triangular envelope to a depth of 75% at a rate equal to the ΔF used for the binaural beats test. The results are shown for 2 cells in Figure 5A and B. Figure 5 plots vector strengths as a function of S/N, and as with the cells shown above, motion resists

the effects of noise. In the same cells, moreover, vector strengths obtained with AM stimuli were no more effective in withstanding noise than were unmodulated stationary tones. This point is summarized for our sample of cells in Figure 6A which plots as a function of S/N, the normalized difference in vector strength between AM tones (r_{am}) and unmodulated tones (r_{stat}):

$$\text{normalized difference for AM} = (r_{am} - r_{stat}) / (r_{am} + r_{stat}) \qquad \text{Eqn. 3}$$

The points in Figure 6A at the lowest S/Ns tend to cluster about zero indicating that an AM tone is not any easier for a cell to detect than an unmodulated tone. At the highest S/Ns tested, AM tones yield lower vector strengths than unmodulated stationary tones ($p < 0.05$, 19 neurons). Similar scatter plots that compare AM tones to leftward and rightward motion at various S/Ns are shown in Figures 6B and C. The equation for the normalized difference is identical to Equation 3, above, except that r_{mot} is substituted for r_{stat}. In these scatter-plots, the points generally fall below zero, indicating that moving stimuli yielded higher vector strengths than did AM stimuli. In a subset of cells, we tested modulation depths ranging from 12.5% to 100% and found results consistent with those described above for 75% modulation.

Discussion

There is a growing body of literature on the neurophysiology of acoustic motion sensitivity. Most of these studies have reported the existence of cells that discharge preferentially for a particular direction of motion in a wide variety of brain areas including the inferior colliculus (e.g. Altman, 1968; Yin and Kuwada, 1983), superior colliculus (e.g. Rauschecker and Harris, 1989; Jen et al., 1987), cerebellum (Bechterev et al., 1975), and auditory cortex (e.g. Sovijarvi and Hyvarinen, 1974; Ahisar et al., 1992;

Stumpf et al., 1992). The recent report by Spitzer and Semple (1991) and the present study address further issues: the effects of motion on auditory spatial resolution and figure ground relationships.

The inferior colliculus is a nearly-obligatory synaptic relay station for ascending auditory information. In this central role, it is likely to process signals that encode a wide variety of acoustic parameters, including the direction and speed of a sound source, for further extraction at higher levels. Our findings in the barn owl suggest that neurons of the ICc are capable of exploiting the motion of sound sources. Tones that mimic a stationary source can be obscured by noise, as judged by a neuron's vector strength, but if the $\Delta\Phi$ changes continuously thus mimicking motion, the neuron's $\Delta\Phi$-specific response re-emerges. The latter could not be observed when the stimulus mimicked a stationary, amplitude-modulated tone-source. The cells also show a higher selectivity for $\Delta\Phi$ in the absence of noise if $\Delta\Phi$ changes *continuously over time than when a* succession of fixed $\Delta\Phi$ values is presented, suggesting that the place-code for space in the ICc is of finer grain for moving sources.

As the phenomena described above were demonstrated with tonal stimuli, they can be subserved by neuronal interactions within a single isofrequency layer. Furthermore, since binaural beats, but not AMs, produce these phenomena, it is likely that the mechanism itself involves interactions between cells that represent adjacent $\Delta\Phi$ values.

Mechanisms and Topographical Maps

In the ICc, $\Delta\Phi$ selective neurons are organized tonotopically, and within each isofrequency lamina there is a topographic representation of $\Delta\Phi$ (Wagner et al., 1987). Recent studies also suggest the existence of a GABA-mediated lateral inhibition within ICc that sharpens stationary $\Delta\Phi$-tuning by suppressing discharge at suboptimal values of

ΔΦ (Fujita and Konishi, 1991). Could the map in an isofrequency lamina of ICc suffice to explain our findings? A neuron's spiking generally continues for a short time after a stimulus is turned off (Wagner, 1990) or leaves the cell's receptive field. Under stationary stimulus conditions this persistence of firing is reflected only in the time domain. With motion, however, the persistence effectively widens the stimulus as it travels across the topographic map by leaving a wake of activity. The moving stimulus would first enter the inhibitory region of the cell's receptive field and, because of its wake, would recruit more inhibitory inputs than would a stationary stimulus, thereby exaggerating the inhibitory trough. As the moving stimulus enters the neuron's excitatory region, it will recruit more excitatory inputs than would a stationary stimulus, thereby exagerating the excitatory peak. Perhaps by placing small phase modulations within selected portions of a cell's complex receptive field we can produce similar effects. The deepened inhibitory troughs may be especially visible against a background discharge evoked by binaurally uncorrelated noise. In the end, a complete model must await considerable anatomical and physiological detail, but it seems reasonable to expect that the mechanisms that sharpen ΔΦ selectivity under stationary conditions can be enhanced to produce the results observed with motion.

Comparisons with Other Neurophysiological Studies

A number of studies in the mammalian auditory system have demonstrated that ΔΦ histograms obtained with continuously changing ΔΦ are narrower than those obtained with stationary stimuli (Yin and Kuwada, 1983; Reale and Brugge, 1990; Spitzer and Semple, 1991). When normalized stationary and binaural-beat histograms are superimposed, it appears that for some mammalian cells the narrowing is due, at least in part, to inhibition at unfavorable ΔΦ values because some values that elicited spikes with stationary stimuli have zero discharge when the stimulus is binaural beats (Yin and

Kuwada, 1983 and Reale and Brugge, 1990).

A recent study by Spitzer and Semple (1991) demonstrates similar effects but also reports an elevated discharge at favorable ΔΦs with motion. Thus they argue for an enhancement of the response at the peak, in addition to a suppression of the response at the troughs. To compare time-averaged spike rates as Spitzer and Semple did, one must assume that a cell's spike rate does not change significantly over the duration of the stationary stimulus. This was the case for the cells shown by Spitzer and Semple (pers. comm.). To evaluate this for our own data we compared maximal spike rates elicited under stationary and motion conditions in two ways. In the first method, we made this assumption of a sustained rate. Thus, for the stationary condition, the spike rate was derived by counting spikes elicited during the entire, one-second tone at the optimal ΔΦ. For motion, we counted the number of spikes elicited as the stimulus moved through the *optimal ΔΦ-bin and divided this quantity by the amount of time (in seconds) spent in the* bin. When these spike rates are compared in a scatter plot, virtually every cell's data point falls above the dotted line that represents equal responses to moving and stationary stimuli (Fig. 7A, rightward motion; Leftward motion gave similar results and is not shown). From this figure it seems clear that motion elicits higher maximal rates. Alternatively, we asked whether each cell could achieve similar maximal spike rates for motion and stationary conditions whether or not these rates were maintained throughout the period of stimulation. Ideally, this analysis would compare maximal instantaneous spike-rates attained under the two conditions. Only a small percentage of our cells, however, fired at rates high enough to allow meaningful estimates of instantaneous spike rates. Instead, we subdivided the optimal ΔΦ-bin for stationary conditions into intervals of 50 msec, which is less time than the moving stimulus spends within the receptive field of most cells. We then calculated a spike rate from the interval with the greatest number of spikes. This analysis is plotted in Figure 7B for rightward motion. These

points tend to disperse evenly above and below the unity-slope line indicating that the motion and stationary discharge rates are not very different. In a few cells with high spike rates, however, motion elicited more spikes even when compared with the latter, more conservative method (Figure 7B), and several other cells showed no response at all to stationary tones but did fire for binaural beats (Figure 7A). The issue of motion and stationary spike rates therefore depends on the time over which averages are taken whether the averaging is done by the experimenter or a post-synaptic neuron.

Comparison with Psychoacoustical Masking Studies

Psychoacoustical studies have shown that simulated motion does *not* enhance the detection of noise-masked signals for man. Wilcott and Gales (1954) masked a bandpassed noise (75 - 850 Hz) with binaurally uncorrelated noise and stepped the interaural delay such as to simulate targets with angular speeds of 6.3, 12.6, and 37.3 degrees of azimuth per second[1]. Detection thresholds thus obtained were compared to those obtained with a similarly masked, stationary signal at a central or eccentric position. These authors found no difference in detectability between moving and stationary targets. More recently, Grantham and Luethke (1988) made similar observations using tones with continuously varying $\Delta\Phi$, masked by binaurally uncorrelated noise. Their studies took care to confine the perceived motion to within the physiological limits of ITD. Compared to the study of Wilcott and Gales (1954), the angular speeds simulated were somewhat higher (173°, 347°, 1730°, and 3472° of azimuth per sec)[1] due to low carrier frequencies and/or high ΔFs. The $\Delta\Phi$ of the stationary signals used for comparison were fixed at 0, $\pi/2$, or π.

When the masker is instead binaurally correlated, the results can be explained

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[1] Computed using Eqn. 1 and assuming a maximal ITD of 650 μsec for humans which results in k = 7.2 μsec of ITD per degree of azimuth (Blauert, 1983).

from what is known regarding the binaural masking of stationary targets (Grantham and Luethke, 1988; Robinson, 1971). With this stimulus configuration, signal detectability is poorest when the signal and masker have similar $\Delta\Phi$s and is better if the $\Delta\Phi$ of the two differ (Jeffress et al., 1952). This is not surprising considering that the binaurally correlated masker would generate a single, well-localized, auditory image at the midline and that the difference in the $\Delta\Phi$ values of the target and noise-masker would dictate the degree of separation between the two auditory images. With tones of continuously varying $\Delta\Phi$, the thresholds are somewhere between the lowest and highest detection thresholds obtained with stationary tones, suggesting that the subjects compute an average from the perceived instantaneous $\Delta\Phi$ values (Grantham and Luethke, 1988). Thus, in man, acoustic motion does not seem to facilitate the detection of masked targets despite the range of speeds, signal types, and maskers tested.

By contrast, there is evidence to suggest that motion facilitates target perception in echolocating bats. Jen and Kamada (1982) demonstrated that two species of echolocating bats, *Pteronotus parnellii* and *Eptesicus fuscus*, are better able to avoid moving obstacles than stationary ones during flight. McCarty and Jen (1983) also showed behaviorally that a bat's ability to discriminate the echo reflected off the target from those reflected off background objects degrades less rapidly with the bat-target distance, if the target moves. Similarly, Simmons (1981) showed that *E. fuscus's* detection threshold for an echolocation signal in noise is lower if the arrival time of returning echoes is jittered, simulating a target whose range fluctuates with time. These behavioral studies in bats and our neurophysiological findings in the barn owl contrast with the negative findings in man. This difference may reflect the more central role played by spatial hearing in the behavior of bats and owls.

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Figure Legends

Figure 1 ΔΦ histograms of 4 ICc neurons (A-D). For each neuron, a stationary ΔΦ histogram (left) and those obtained with leftward (center) and rightward (right) motion are shown. Negative ΔΦ values indicate that the tone in the left ear led. The vector strength, r, is shown at the top right of each histogram. The stationary histograms were normalized to the highest response. The motion histograms were normalized to the highest response obtained in either of the two directions. The carrier frequencies and the ΔFs are as follows: A 7692 Hz, 2 Hz; B 2000 Hz, 1 Hz; C 2000 Hz, 1Hz; D 5555 Hz, 1 Hz.

Figure 2 Response of an ICc neuron to tones in noise. ΔΦ histograms were plotted for stationary stimuli (left column) and rightward motion (right column) at S/Ns of 10.0 (A), 0.4 (B), 0.2 (C), 0.1 (D), and 0.05 (E). Binaural beats simulating leftward motion yielded histograms similar to those from rightward motion and are not shown. The spike rate is normalized to the maximal rate found in each column. The vector strength, r, is shown to the upper left of each histogram. The motion vector strength degrades less rapidly than the stationary vector strength as noise is added. Carrier frequency = 6667 Hz, ΔF = 4 Hz.

Figure 3 Plots of vector strength as a function of S/N for four ICc neurons. The graph shown in A was taken from the cell whose response was depicted in Figure 2. Graph D is taken from the cell depicted in Figure 1D. Carrier frequencies and ΔFs are as follows: A 6667 Hz, 4 Hz; B 4762 Hz, 1 Hz; C 2564 Hz, 8Hz; D 5555 Hz, 1 Hz.

Figure 4 Scatter-plots of normalized differences in vector strength as a function of S/N. The difference between the vector strengths obtained under motion conditions and stationary conditions normalized to the sum of the two (see Eqn. 2) is plotted as a function of S/N. Positive values indicate that motion produced higher vector strengths. A leftward motion; B rightward motion.
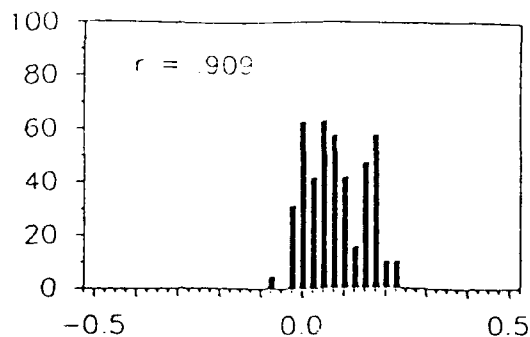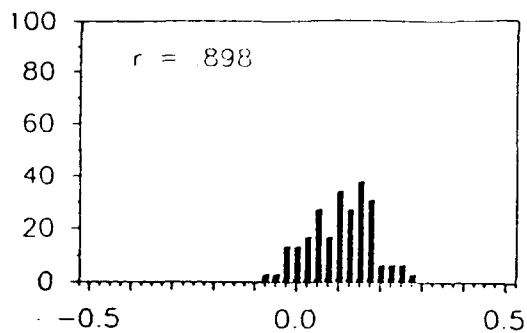
Figure 5 Comparisons of AM tones, unmodulated tones, and binaural beats in noise. Vector strengths obtained with motion (triangles), unmodulated stationary tones (filled circles), and AM tones (unfilled circles) were plotted as a function of S/N for 2 ICc neurons (A, B). Both plots show that vector strengths recover from the obscuring effects of noise most rapidly with motion, and that an amplitude-modulated stationary tone is no better than an unmodulated stationary tone. In fact, AMs tend to yield lower vector strengths at the high S/Ns as seen in B. Curves obtained with leftward motion were comparable to those obtained with rightward motion and are not shown. Modulation depth was 75%. Carrier frequency, ΔF: A 6667 Hz, 1 Hz; B 3000 Hz, 1 Hz.

Figure 6 Comparison of AM tones with unmodulated stationary tones and with binaural beats for our sample. Positive values indicate that AM tones yielded higher vector strengths. A: The normalized difference in vector strength between stationary AM tones and stationary unmodulated tones (Eqn. 3) is plotted as a function of S/N. AM tones tend to yield similar vector strengths to that of unmodulated tones at low S/Ns. At high S/N, the vector strengths obtained with AM are lower. B and C: Normalized difference in vector strength between stationary AM tones and leftward (B) and rightward (C) motion. Vector strengths with AM tones are uniformly less than those obtained with motion.
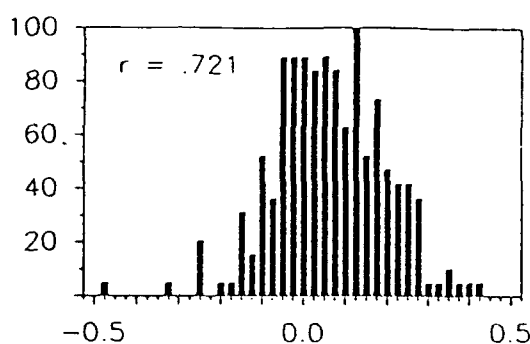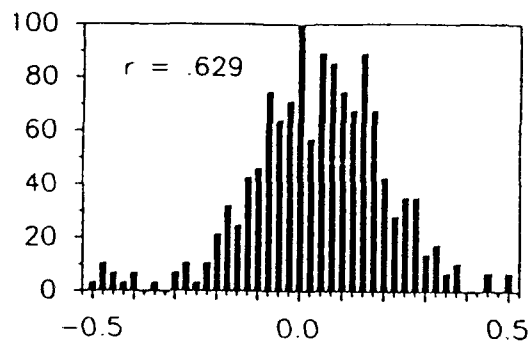
Figure 7 Scatter-plots of maximal firing rates obtained with binaural beats graphed as a function of stationary firing rates. The dotted lines have a slope of 1. The motion spike-rate is the quotient of the number of spikes in the optimal $\Delta\Phi$ bin divided by the amount of time (in seconds) spent in that bin by the moving stimulus. In A, the stationary spike rate is the number of spikes obtained with the stimulus fixed at the optimal $\Delta\Phi$ for one second. This comparison clearly shows higher spike-rates for moving stimuli. A few cells do not discharge at all for stationary stimuli. In B, stationary spike rates were calculated from the highest spike rate observed after subdividing the response to the 1-sec, stationary tone into 50-msec intervals. This comparison shows that motion and stationary stimuli tend to elicit comparable firing rates. Cells that did not discharge for stationary tones were excluded from B.

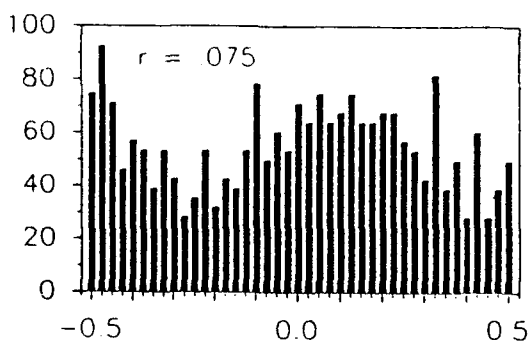Stationary   Leftward   Rightward

A   r = .31   r = .82   r = .75

B   r = .30   r = .71   r = .76

C   r = .89   r = .96   r = .94

D   r = .92   r = .83   r = .85

% maximal spike rate

interaural phase difference (cycles)

FIG 5
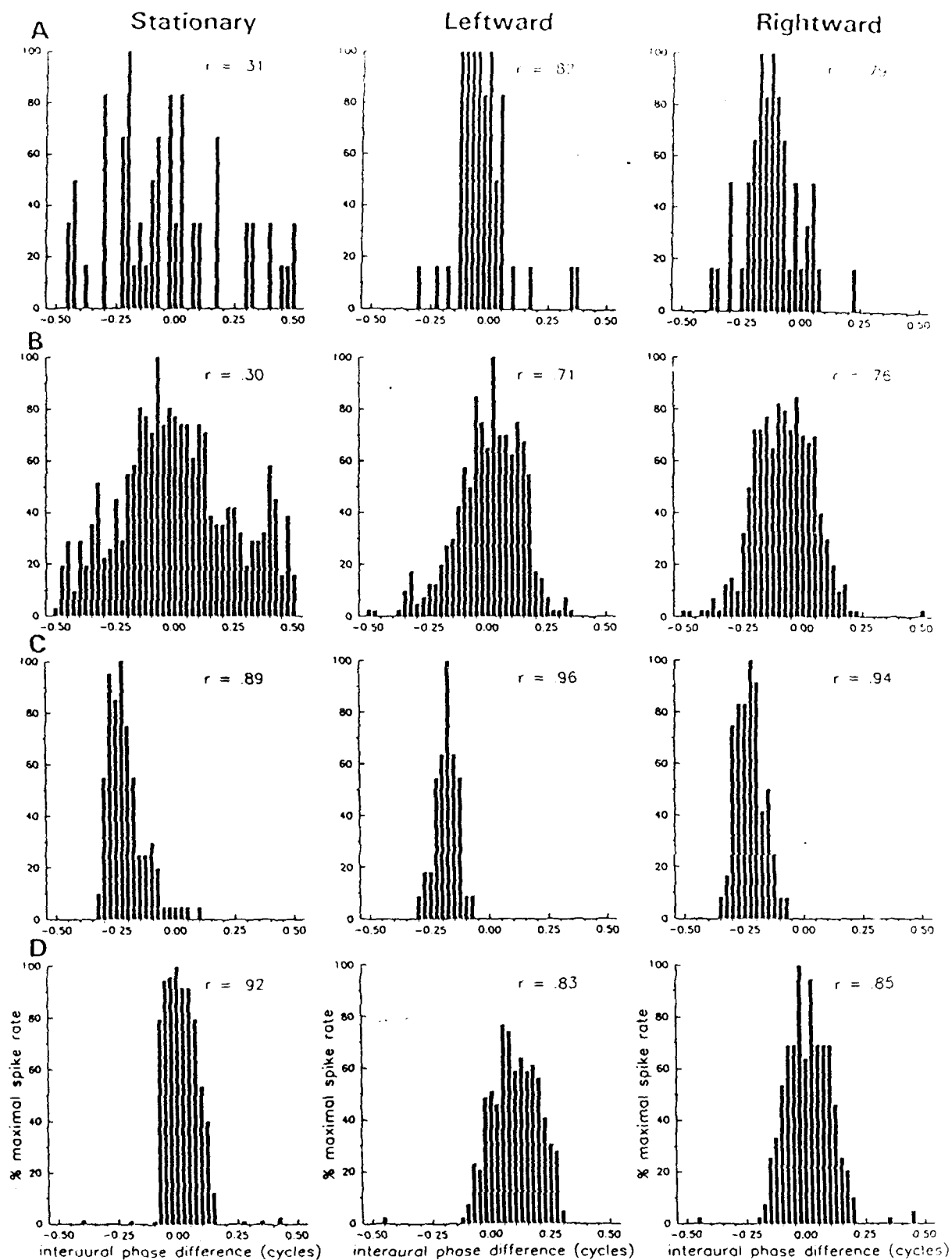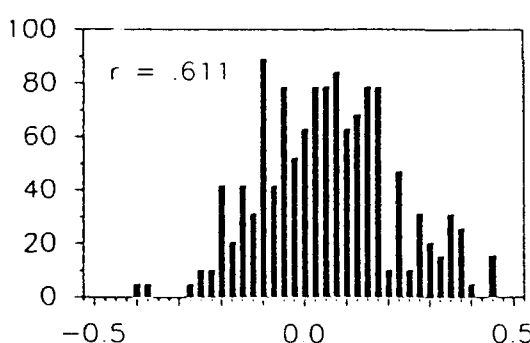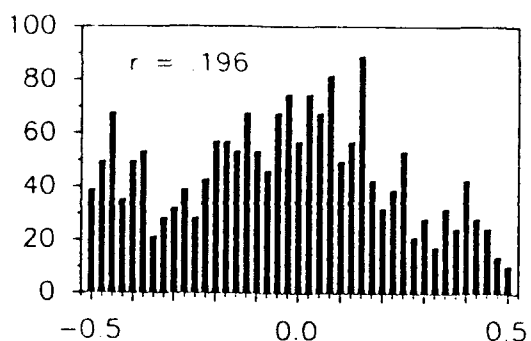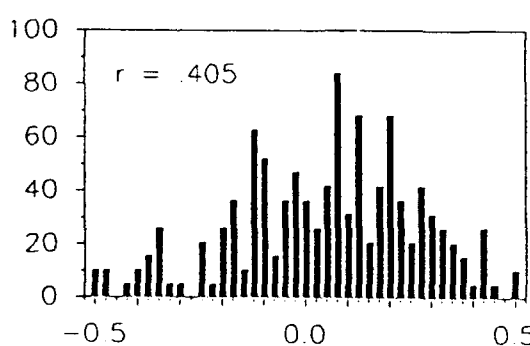
FIG 5
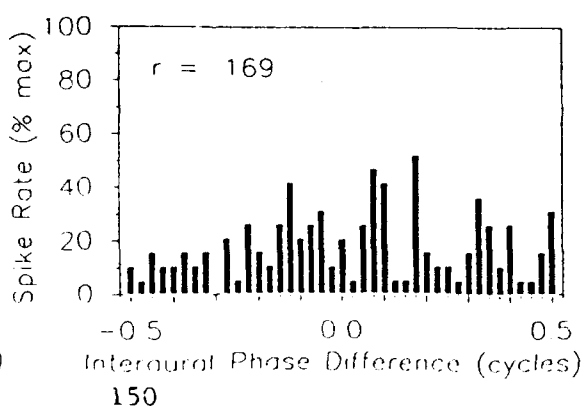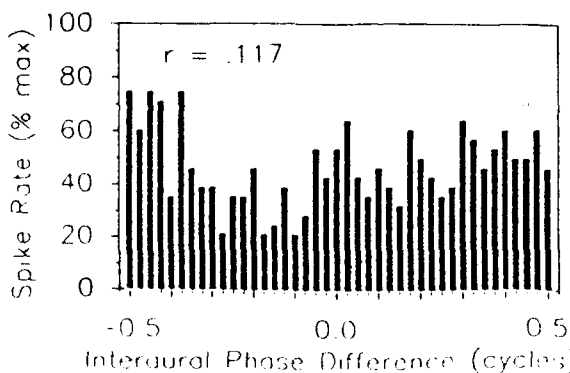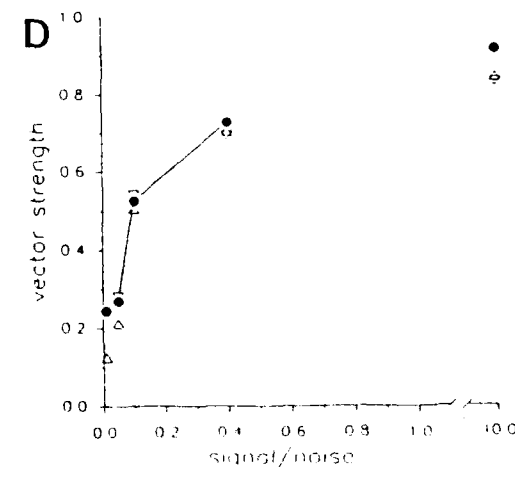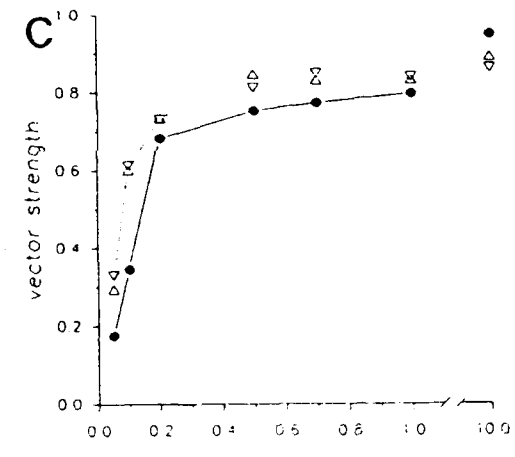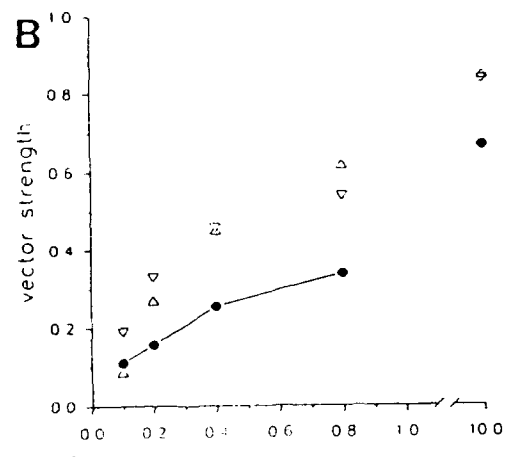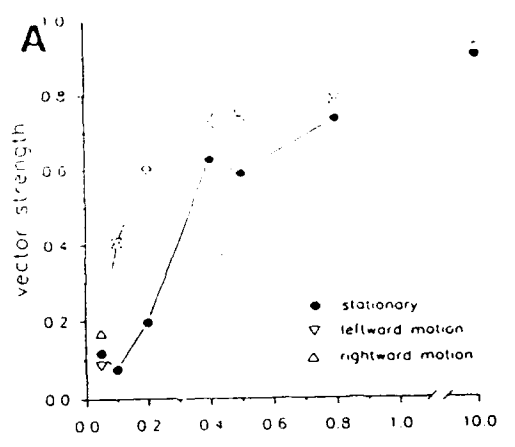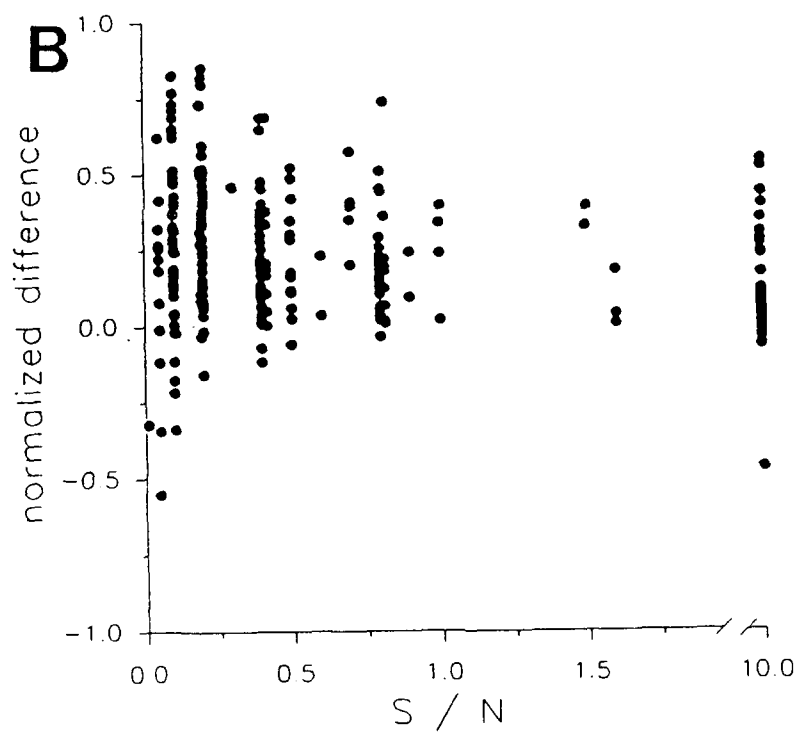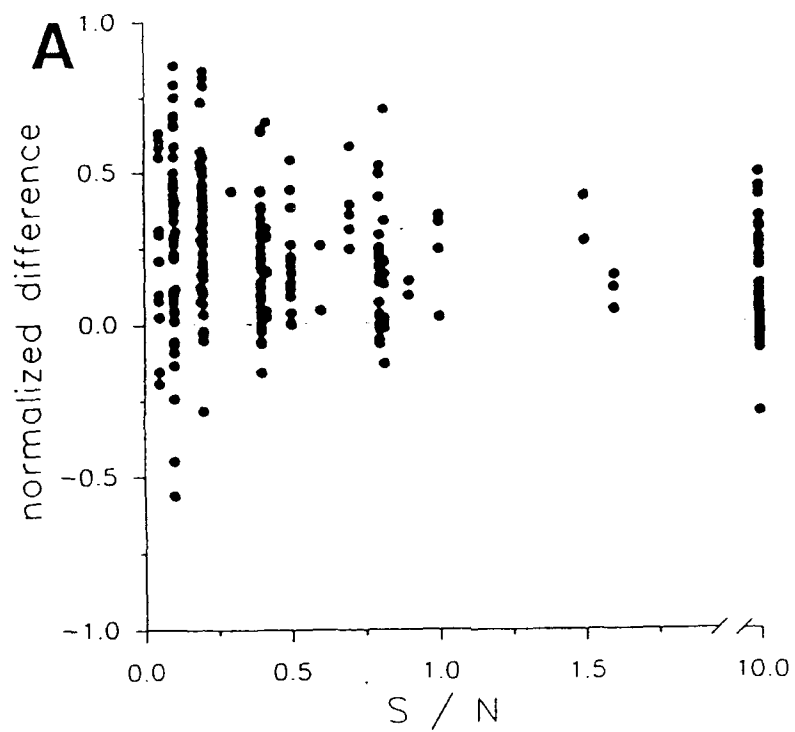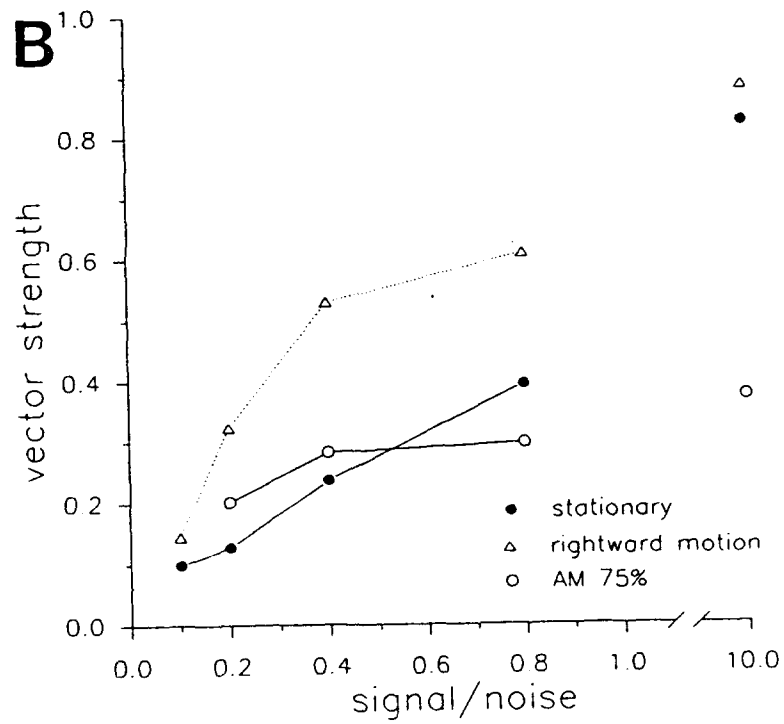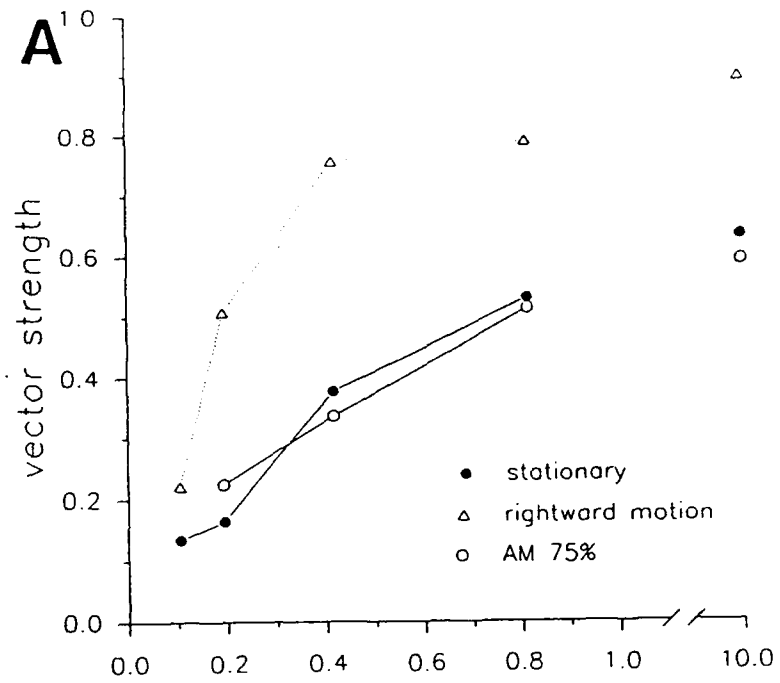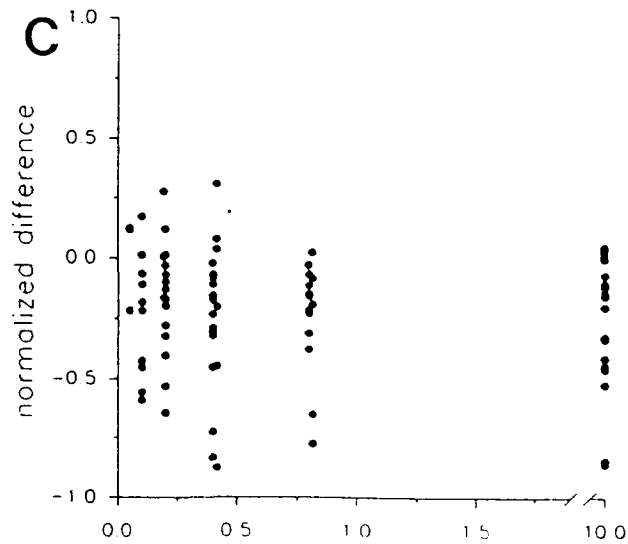
DISCRIMINATION OF TARGET DISTANCE FROM SOUND ALONE

BY THE BARN OWL, Tyto alba

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Few investigators have examined the ability of any animal to localize sounds in depth passively. This may, in part, be due to the poor ability of humans at such a task (see Middlebrooks and Green, 1991, for review). We are conducting preliminary tests of the ability of barn owls to discriminate distance from sound alone.

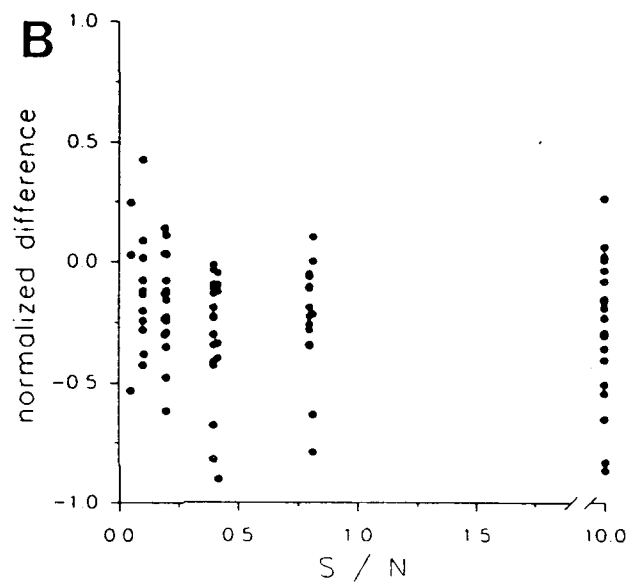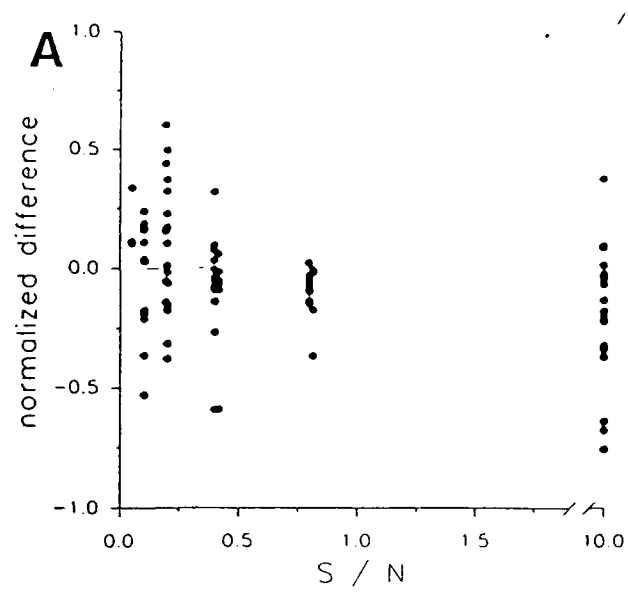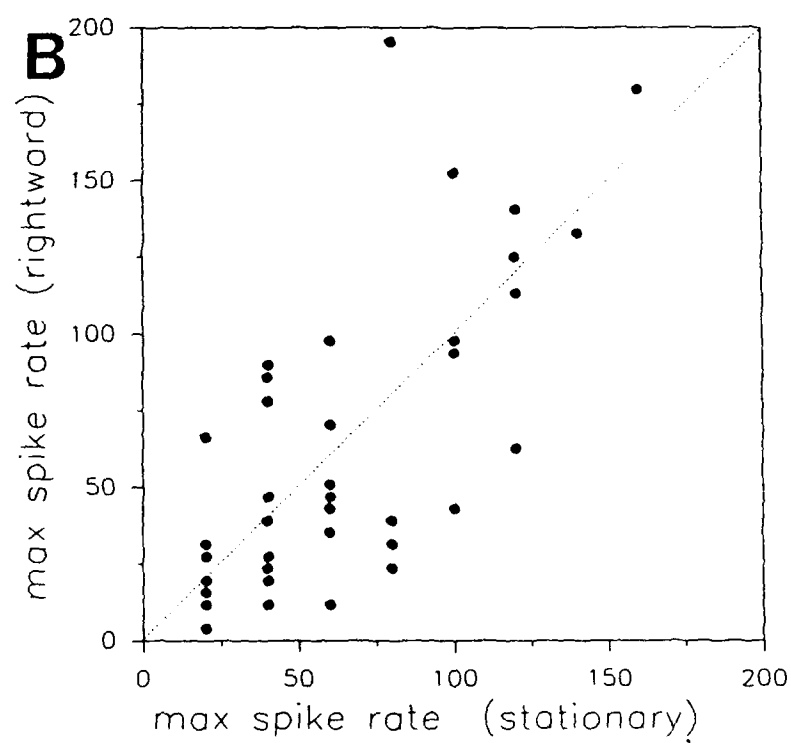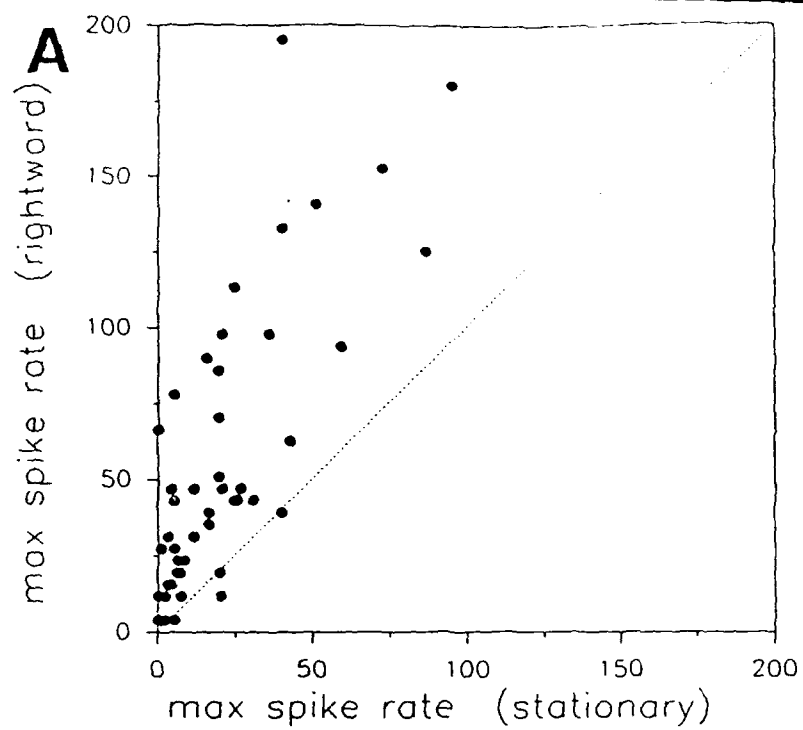If the intensity of a sound at the source is known, the distance to the source can be judged by it's relative intensity. Intensity decreases as the first power of distance (Coleman, 1963). Thus a listener's ability to discriminate the relative distance to two identical sound sources might be related to and limited by their ability to discriminate intensity differences. The limit of human's ability to discriminate the intensity of a broadband noise is between 0.3 and 0.5 dB (Miller, 1947), which corresponds to a difference in distance of between 3.5 and 6 percent. Strybel and Perrott (1984) have demonstrated that this expected limitation to distance acuity was met for comparison of two sounds when the reference sound was more than 3 meters away. At shorter distances, distance acuity was worse than intensity acuity would predict.

There are other potential cues for auditory distance perception as well (see Coleman, 1963 for review). For example, near to the source, where the sound source appears spherical, low frequencies are more greatly attenuated. More distantly, high frequencies are preferentially attenuated. In echoic environments, the perceived sound is that which is directly incident combined with any reverberant sound. The ratio of direct to indirect sound changes with distance as well as with the qualities of the particular

listening environment. Binaural cues are available as well, e.g. both interaural phase and intensity differences decrease with distance in a frequency dependent manner.

Apart from a few inconclusive studies on humans and the extensive work on active depth perception by echolocation in bats and other animals, there seem to be no studies of auditory depth perception in other vertebrates. The barn owl, however, can catch its prey in total darkness and must necessarily recognize the distance to the prey (Payne, 1971). It seems likely that the owl's determination of distance relies, at least in part, on auditory cues. For these reasons we have begun an investigation of the owl's ability, and the cues necessary, to discriminate depth from sound alone.

Barn owls tend to orient their head towards novel sounds and, in some cases, will visually accommodate to the depth from which the sound originates. We use this behavior as an assay to quantify the owl's ability to discriminate depth by sound alone. A barn owl is placed in a mesh-cage (ca. 30 X 30 X 30 cm.) within a large, dimly lit room that is padded with anechoic foam. A sound is then presented to the owl from one of a number of loudspeakers arrayed in depth between 1 and 4 meters away from the owl. Typically, the owl will orient it's head towards this sound.

We ascertain the owl's ability to localize the sound in depth by judging the state of accommodation of its eyes. To this end, a photoretinoscope (Schaeffel, et al. 1987) is mounted on the lens of an infra-red sensitive video camera, located about 2 meters from the bird in approximate alignment with the array of speakers. When the bird's eye is focused to a point nearer than the video camera, the video image of the eye is characterized by a dark region occurring in the upper half of the eye (Figure 1). In contrast, when the eye is focused at a distance greater than that of the camera, the dark area occurs in the lower half of the eye (Figure 2). Further quantification of the point of focus is also possible by estimation of the size of the dark fraction. The speaker array provides no non-auditory cues as to the distance of the sound from the owl. To encourage the owl to perform this behavior we reward it with food after a successful trial.

Thus far, we have shown that the bird can discriminate sounds that appear to

move across the speaker array towards the bird rather than away from the bird. Of course, the loudness of the sound changes as the sound "moves" across the speaker array, and a serial comparison of sound loudness would make this task relatively easy. We have succeeded in training one bird to orient in depth to single presentations of a sound, thus eliminating the possibility of serial comparison. As other birds have yet to demonstrate this ability we are not yet confident of what the bird is attending to. A major problem to date is keeping the bird adequately motivated to perform the task. We will continue with these tests.

The most robust responses thus far, however, occurred in our initial "pilot" experiments. A bird was placed in a cage on the floor and a motorized, radio-controlled target was run toward or away from the bird. Each of two birds tested, successfully discriminated in the dark between this advancing or receding noisy object. The success of these pilot experiments inspired what will be our next approach. We will test whether an owl can make the same discrimination when the **recorded sound** of the advancing or receding race car is played through a **stationary loudspeaker**. If this discrimination is possible, we will selectively eliminate some of the cues from these recordings until the bird can no longer successfully discriminate.

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Schaeffel F, Farkas L, Howland HC (1987) Infrared photoretinoscope. *Applied Optics* 26:1505-1509

Strybel TZ, Perrott DR (1984) Discrimination of relative distance in the auditory modality: The success and failure of the loudness discrimination hypothesis. *J Acoust Soc Am* 76:318-320
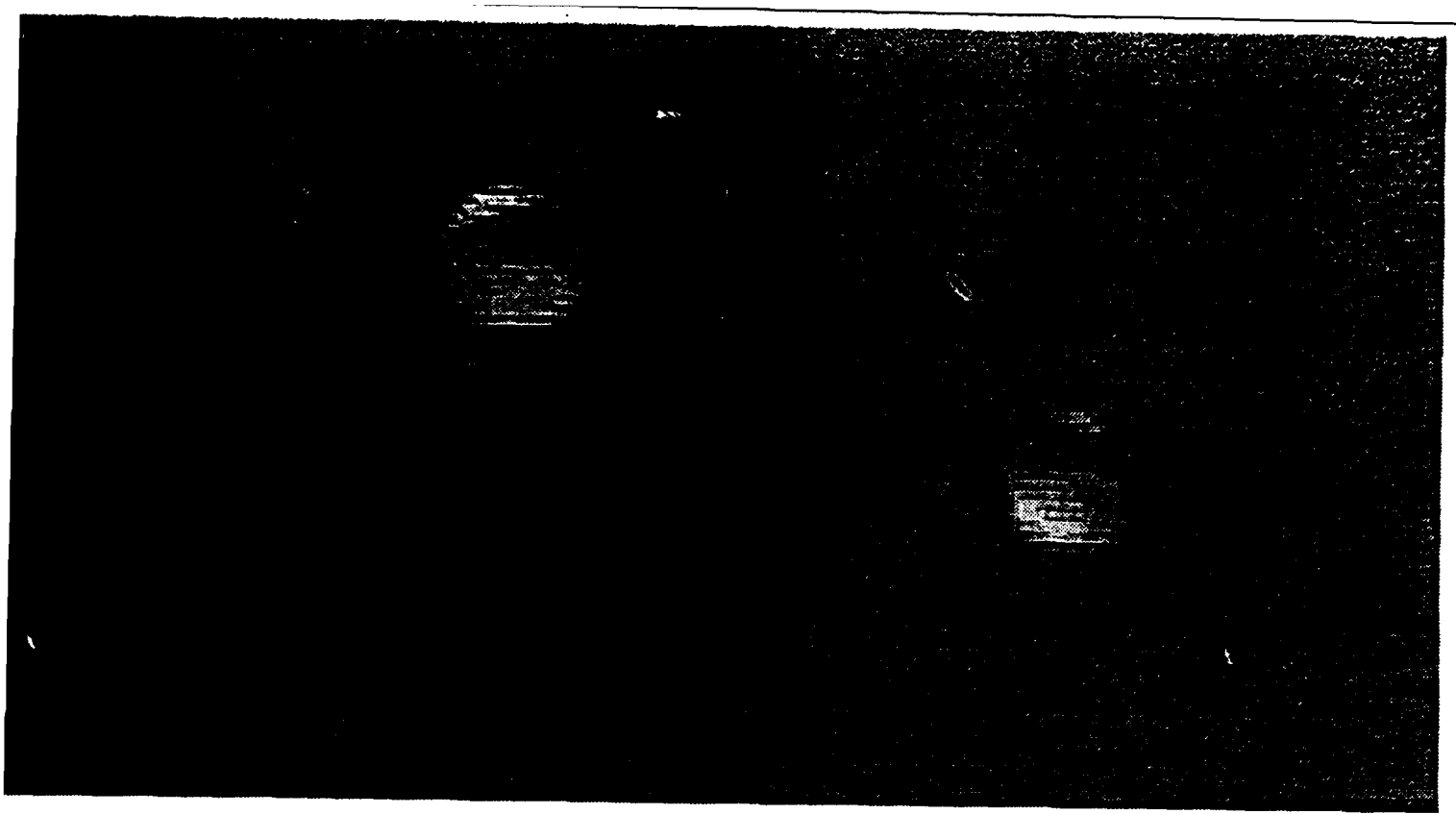
Figure 1. Photoretinoscopic image of the barn owl's eyes when the eye's are focussed at a point that is closer than the camera. A dark region appears in the upper portion of the image of the eye. The owl was looking towards a sound emitted from a loudspeaker that was located between the camera and the bird.
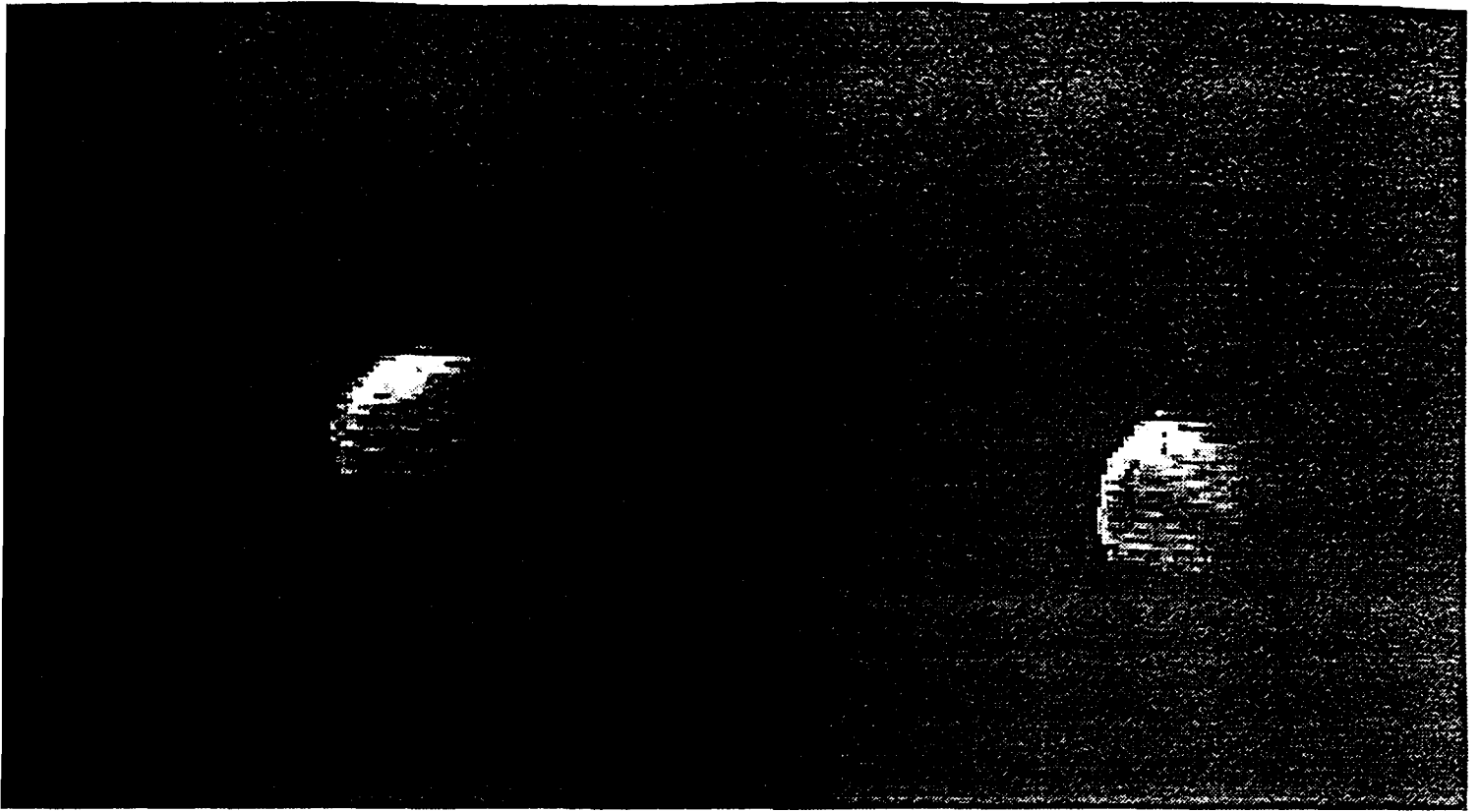
Figure 2. Photoretinoscopic image of the owl's eyes when the photoretinoscope is located between the point of focus and the bird. A dark region appears in the lower portion of the image of the eye. In this case, the active loudspeaker was more distant from the bird than was the camera.

Imaging of Multiple Acoustic Targets
by a Neural Network

Technical Progress Report
to the
Institute of Neuroscience
University of Oregon

Terry T. Takahashi, Michael K. Flemming, and Will Goodwin

Fall 1991

Background:

The auditory system of the barn owl contains a topographic, visual-system-like map of space by which the owl orients rapidly and accurately toward a sound-source. Its errors are less than one degree in the vertical and horizontal axes. The basic units of this topographic display is the space-specific neuron an auditory neuron with a spatial receptive field. The space-specific neuron has a spatial receptive field because it is selective for a narrow range of interaural time and intensity differences, the binaural cues that co-vary with the horizontal and vertical co-ordinates of a source respectively.

The map of space is found in the external nucleus of the inferior colliculus (ICx), a region of the midbrain, and receives its inputs from the central nucleus of the inferior colliculus (ICc). The ICc too is spatiotopically arranged, except that its map represents only the horizontal axis and its neurons represents interaural time difference (ITD) as a tonotopically organized ensemble of neurons. Within each ensemble, cells are selective for interaural phase difference (IPD) and for a narrow band of frequencies. Such phase-sensitive cells cannot by themselves discriminate between a particular value of ITD and ITDs that differ by integer multiples of the stimulus period, and therefore cannot specify a unique ITD. However, the preferred IPDs and frequencies of the cells within the ensembles are linearly related. A linear relationship between IPD and frequency means that an ITD is represented by the ensemble *as a whole*. These ensembles are arranged systematically in the ICc such that a map of ITD (and therefore azimuth) is formed. Axon-tracing techniques have demonstrated that an ensemble thus representing a certain ITD innervates space-specific neurons in the ICx that are selective for that same ITD.

Natural acoustic environments usually contain many sources of sounds, and in order for such maps to function effectively, each source must give rise to a corresponding focus of neural activity. While this is a simple task for visual or somatosensory maps, the auditory system faces the complication that the sound waves from multiple sources sum, vectorially, at the ear drums. Take for instance, two speakers, both broadcasting the same pure tone. The left and right ear drums would

vibrate as though it were stimulated by a single sinusoid the amplitude and phase of which would be the vector sum of the sine wave from each source. A single phantom source is heard, somewhere between the actual locations of the two real sources. There is no physical way in which to parse this stimulus into two sources. However, if the sources broadcast complex signals with some spectral components unique to a source and others that might be shared, it becomes possible to discriminate two sources and to produce two corresponding points of neural activity on the map of space.

Given the physiological capabilities of its constituent cells, can the owl's space-map parse multiple targets accurately? Recent neurophysiological data suggest that the ICc of the barn owl contains many lateral connections that, among other things, makes the map suitable for the detection of acoustic motion in a noisy background and for the determination of acoustic-motion direction (ms enclosed). Such lateral interconnections may also be useful for the suppression of phantom images that would be generated by multiple sources broadcasting signals with overlapping spectra.

Current Work:

Current support from the ONR allowed us to begin work on a neural network that parses multiple, simulated, acoustic targets into corresponding neural images on an auditory space map. The input neurons are modelled after the cells of the ICc from which we have been recording, and are arrayed in tonotopic ensembles, as they would be *in vivo*. Each input neuron is connected directly to all cells in the output layer, at first, with random weights (Fig. 1). The weights are changed as a result of training, in which the computer generates two sound-sources at random locations along a one-dimensional space and the network's task is to generate hotspots of activity on a similar output map. The "sound" from each source is a sum of randomly picked sinusoids having random starting phase angles. The computer computes the waveform that a set of left and right eardrums might receive, given the spectrum and location of each source along the horizontal meridian, then activates the appropriate units in the input layer. Differences

between the correct answer and the results of the output layer are corrected by standard back-propagation algorithms.

Training takes less than 1000 iterations (about 20 minutes on our SPARC-2 workstation [Sun Microsystems]), and the network, with its final connectional weights established, graphically generates hotspots of activity on the output layer (Fig. 2A-C, top window - "OUTPUT UNITS"). Targets can be presented to the trained network by the user who can specify the spectra and positions of the two sound-sources and the network reacts in real-time (Fig. 2A-C, center window - "SOURCE HISTOGRAMS"). The number of hotspots displayed by the network is accurate when the sources have no common frequencies (Fig. 2A) and tends to remain so even when the two targets brodcasts frequencies in common (Fig. 2B). Of course, if the spectra of the two sources are identical, the network will display only a single hotspot (Fig. 2C).

Most interestingly, an analysis of the connectional weights of a fully trained network revealed that the input layer, which simulates the known properties of ICc cells, connects with the output layer in a manner suggestive of the ITD-sensitive cells of the ICx. A particular output unit, like an ICx neuron, receives *excitatory inputs from ICc cells* of differing best frequencies whose IPDs are related to a particular ITD value. Input units that are not phase-equivalents of the ITD inhibit that output unit.

The similarity between the final network's connectivity and the architecture of the owl's inferior colliculus suggests that the owl's auditory system, like our network, should be effective in parsing the auditory scene. This is not surprising considering that in its complex natural environment, the barn owl can hunt by passive hearing alone.

Applications:

Our network will allow us to model the possible ways in which the acoustic images are built and represented by the nervous system. It can generate testable hypotheses on how animals, and even machines, can attend to specific stimuli in a noisy environment.

There are also more direct applications. If expanded to two dimensions, our network will form a visual display for acoustic sources. Each sound-emitting target would be represented by an active area on this map. Such a representation may allow a human operator to keep track of acoustic targets visually, over time, thus making use of the superb capability of the human visual system to detect patterns. A more unorthodox application is the possibility of detecting silent objects. Once numerous sound-sources in an environment are displayed on our space-map, a silent source that occluded some part of the displayed scene would cast a shadow and may therefore be detectable. Because of the topographic nature of the map, the dimensions of the object might also be discernable. Such scenario, of course, would depend on the accurate mapping of many sources.

Future Work:

1. In order to make our network more capable, we need further biological data. What kinds of acoustic features are most effectively parsed by the owl's space map? How much spectral similarity between multiple targets can the owl's space map tolerate before it is unable to suppress phantom images? How will the space map deal with multiple targets whose sounds vary across time by movement or by amplitude modulation? To address these questions we intend to reconstruct the electrical activity in the inferior colliculus that result from multiple, concomitantly-active speakers. The stimulus parameters will be varied and the reconstructed electrical activity compared.

2. In addition to the incorporation of new biological data we intend to develop the network itself in the following ways:

    1. Make the network capable of utilizing real-world sounds, received through a pair of microphones and processed by a spectrum analyzer. The spectrum analyzer will compute the inter-microphone phase and amplitude differences for each frequency band, and the analyzer's output will be fed to our network over a
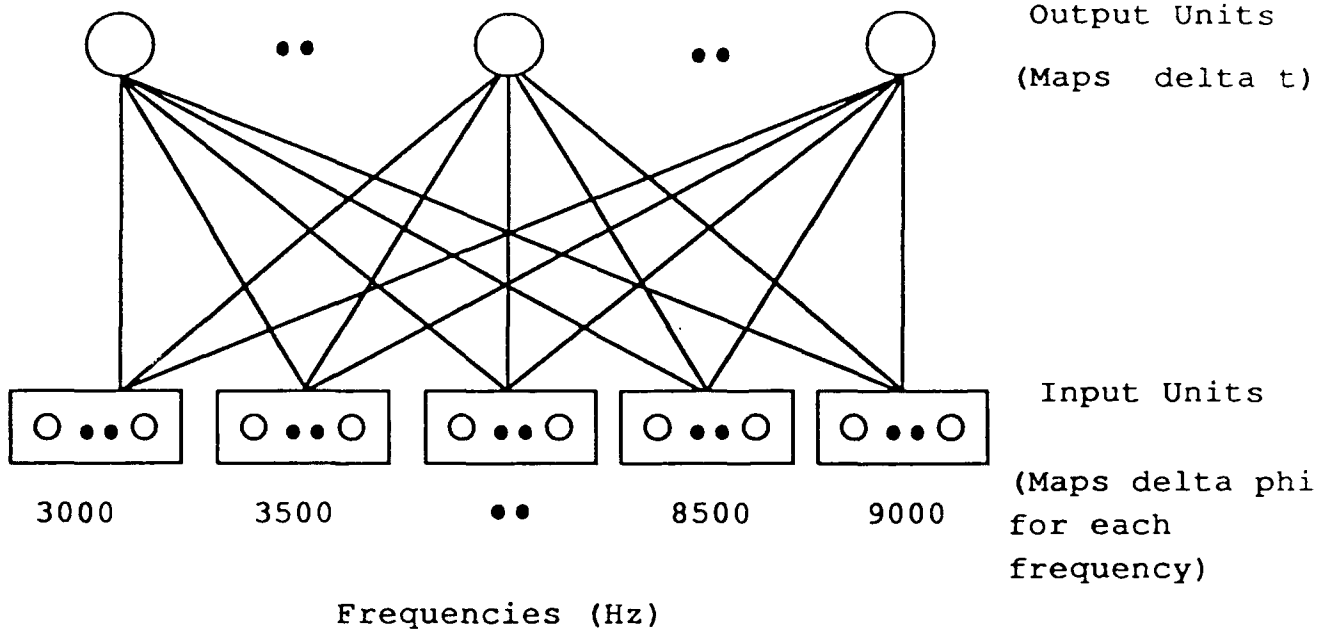
Sun-GPIB interface.

2. Train the network to recognize any number of sound-sources. Interestingly, our current network, trained to parse two targets, has recently been found to be capable of parsing three targets, under some conditions.

3. Expand the network from a 2-dimensional representations that can take inputs from a pair of vertically separated microphones and a pair of horizontally separated microphones.
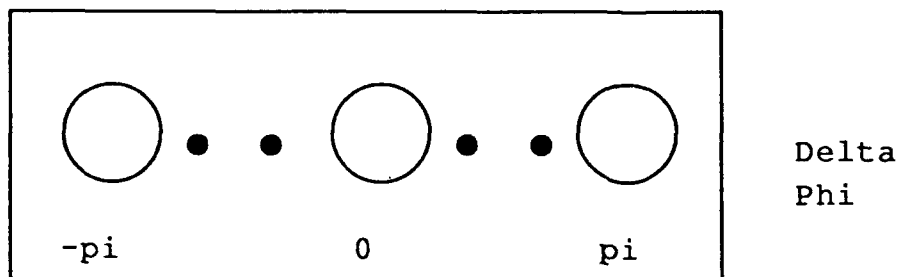
Figure Captions:

Figure 1 Network organization. The top schematic diagram shows the relationship between input and output layers. The large circles at the top represent 3 of the 25 output units and each output unit represents a certain interaural time difference (ITD). Each out put unit is connected to every unit of the input layer. The input layer is organized such

Figure 2 User interface. Photographs A and B depict the user interface under different conditions. In each, the top center window, labeled "OUTPUT UNITS" displays the one-dimenstional map of space onto which the network projects the images (black squares) it has parsed from the input. The center window, labeled "SOURCE HISTOGRAMS", depicts the location and spectrum of the two sound-sources specified by the user. The lower two windows with colored bars are higher-magnification versions of the two sources' spectra. Lower frequencies are represented to the left of higher frequencies and the height of a bar indicates the amplitude of a particular spectral component. In A, the spectra of the two sources contain different frequencies and the network parses them into two targets as depicted by the two black squares in the top center window. In B, the signals from two sources contain a number of common, but the network is still able to correctly parse the number of targets, although localization is not precise. If the signals from the two sources are identical (not shown) the network indicates a single, phantom source between the locations of the actual sources.
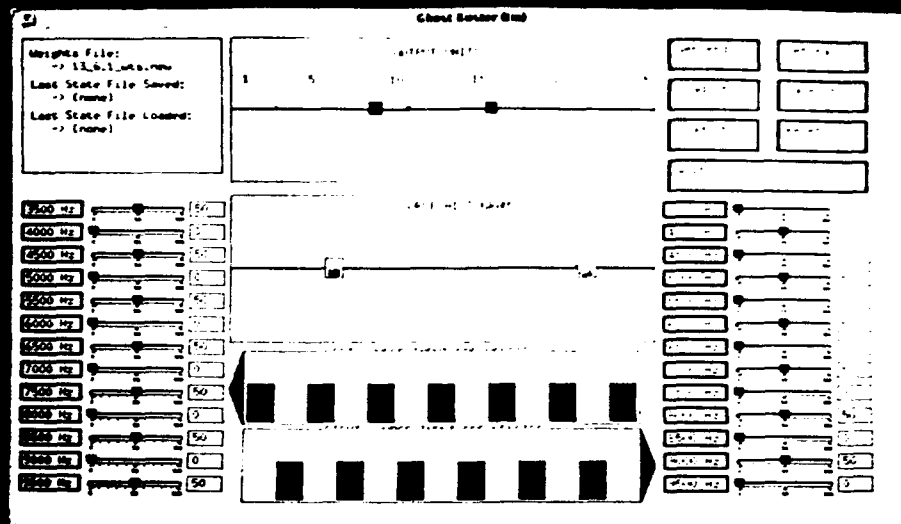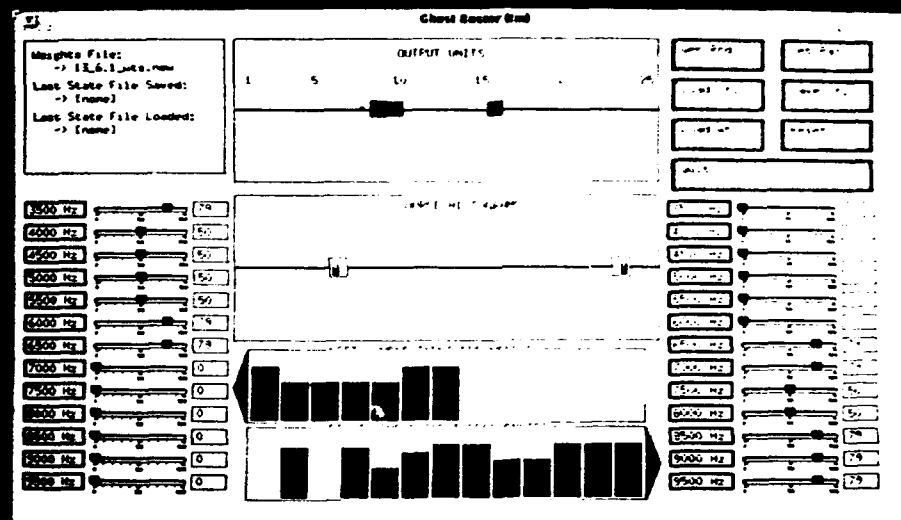
Positions

Output Units

(Maps   delta t)

Input Units

(Maps delta phi
for each
frequency)

3000   3500   ••   8500   9000

Frequencies (Hz)
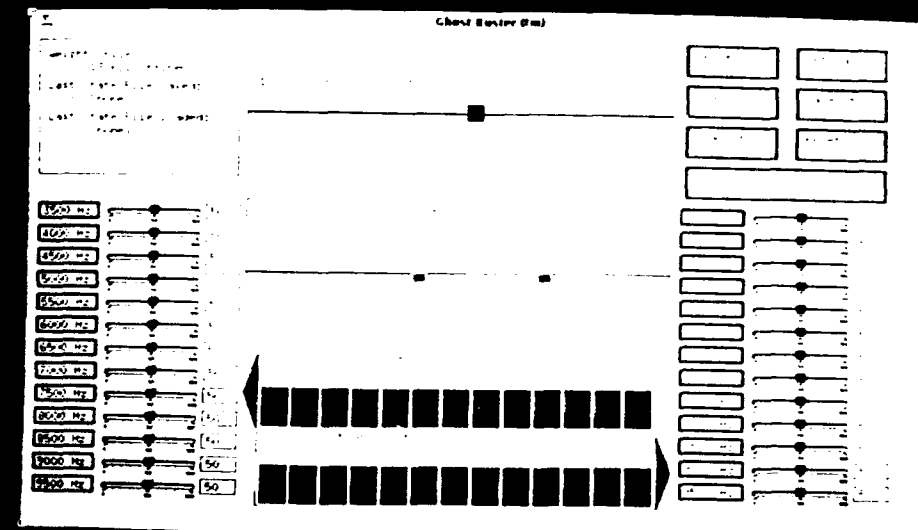
Frequency Set

Delta
Phi

-pi   0   pi

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2nd topic title Neuroethology
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Special Requests (e.g., projection requirements)

TOPOGRAPHIC REPRSENTATION OF MULTIPLE ACOUSTIC TARGETS BY A NEURAL NETWORK. MK Fleming, WJ Goodwin, and TT Takahashi*. Dept of Psych., Stanford Univ., Stanford, CA & Inst. of Neurosci., Univ. of Oregon, Eugene, OR.

The barn owl's inferior colliculus contains a visual-system-like map of space built from auditory units with spatial receptive-fields. Visual maps can easily represent more than one stimulus. In the auditory system, however, sound-waves from multiple sources will sum at the eardrums, and, if two or more sound sources broadcast common spectral components, the binaural cues for the shared components, such as interaural phase and intensity differences, assume values that are the vector averages of those frequencies from the individual sources. For an auditory space-map to represent multiple targets accurately, other cues are therefore required. We investigated whether the owl's auditory space map could represent two acoustic targets, given that the two targets had some unshared spectral components. Using standard back-propagation algorithms we trained a two-layered network to parse simulated sound-sources into hotspots of neural activity along a one-dimensional space map. The input layer consisted of units, which, like the cells of the central inferior collicular nucleus (ICc), were selective for a frequency and an interaural phase difference ($\Delta\Phi$). Simulated sources at given spatial loci can be represented as a spectrum of $\Delta\Phi$s by this input layer. The output layer, like the external inferior collicular nucleus (ICx), consisted of neurons that were selective for a particular $\Delta\Phi$ spectrum. Following training, the network was capable of accurately representing the targets' number and locations on the one-dimensional space map, provided that the simulated sources broadcast some unshared frequencies and that shared frequencies were represented with differing amplitudes. Most interestingly, analysis of the connectional weights revealed a projection pattern between input and output layers that was strikingly similar to the known connectivity between the ICc and ICx in the owl.

KEY WORDS: (see instructions p. 4)

1. sound localization
2. inferior colliculus
3. owl
4. back-propagation

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Publications
Fleming, M.K. and Cottrel Facial recognition. (Presented at the Berkeley-Stanford Symposium on Facial Recognition) *IJCNN* Abstract.
Fleming, M.K., W.J. Goodwin, and T.T. Takahashi 1992 Topographic representation of multiple acoustic targets by a neural network. *Abst. Soc. Neurosci.*

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Consulting Software Engineer

I have extensive experience in many areas of software development, mathematics, and teaching. I have held research assistant positions in the Psychology and Linguistics Departments at the University of Oregon. Currently, I have a research assistant position in the Institute of Neurosciences at the University of Oregon. In these positions I was involved in the development and design of a variety of experiments in the areas of auditory systems, human vision and natural language acquisition. It was my responsibility to implement, modify, update, and maintain the software for stimulus preparation, experimental control, statistical analysis, and mathematical modeling of the psychophysics. I am currently working on a neural network which models some of the auditory mechanisms of the barn owl.

My software experience includes work with the Macintosh, MS-DOS, the Symbolics 3600 LISP Machine, Sun Workstations, UNIX, real-time interrupt driven systems, experimental control and analysis for human vision and natural language studies, and implementation of many mathematical algorithms. I am proficient in C, LISP, Pascal and Fortran. In addition, I have experience with C++ and Object C as well as Object Pascal. I have worked on both large and small software projects including working with end users to design, build and deliver the desired project.

Education

M.S. in Computer and Information Science
University of Oregon, 1985

M.S. in Mathematics
University of Arizona, 1976

B.S. with Major in Mathematics and minor in Physics,
Honors College, magna cum laude,
Western Michigan University, 1973

Work Experience

September 1991 to present
Research Assistant, Institute of Neurosciences, University of Oregon

I have been working with Dr. Terry Takahashi in the Neurosciences Department at the University of Oregon. Dr. Takahashi has been studying the hearing mechanisms of barn owls. I have been developing a back propagation neural net model of the barn owl's auditory location system. I have also been administering the Sun Unix workstation in Dr. Takahashi's lab. This project has involved working with several graduate students and post-doctoral students as well as Dr. Takashi. I am extending the neural network model to be a flexible modeling tool which can be used for other modeling purposes. The model is also being extended to include the ability to train the network with both actual auditory recordings as well as randomly generated inputs.

Languages : C, UNIX

March 1990 to June 1990, and March 1991 to present
Research Assistant, Linguistics Department, University of Oregon

I worked with Dr. Tom Givon and one of his graduate students to design and implement a series of experimental paradigms to investigate the study of natural language processing and acquisition. I wrote the software to control the experiments, and create the stimuli for use in the experiments, and some preliminary analysis of the data. The experimental stimuli included text, visual, and auditory stimuli. All of this work was done on the Macintosh. I have been responsible for the modification and update of the software in an ongoing basis.

Languages : Think Pascal, Hypercard

September 1985 to August 1991
Research Assistant, Psychology Department, University of Oregon

I worked with Dr. Jacob Beck and several graduate and undergraduate students in studying certain processes involved in the human visual system. In particular, we investigated the perception of a three dimensional surface and its relation to several types of projections onto a flat two dimensional surface (ie. paper or computer monitor). Another topic of interest has been image segregation based on texture differences. In both of these projects, I was responsible for the development of the mathematical algorithms which are used to model these processes in the visual system, and the implementation and maintenance of the software which is used to run the simulations of these processes, create the displays used in the experiments with human subjects, collect and analyze the data, and control the experiments. The mathematical algorithms have utilized among others, three dimensional geometric transformations, surface gradients, and convolutions utilizing the Fast Fourier Transform. This work has been done primarily on a LISP machine. Some work has been done on a Macintosh. ### Languages : LISP, Think Pascal, Think C.

January 1991 to June 1991
Consultant to Maxima Software, Eugene, Oregon

I have worked on adding features to a system which was developed under SCO Unix. I made modifications to and added new features to the file system functions. In addition, I did the majority of the work on adding the capability of doing a complete coredump in response to a fault condition. A core image was compressed and written to a floppy disk in a form compatible with the debugging tools available in the Unix environment. ### Languages : C

May 1989 to December 1991

Consultant to Spectra Physics, Eugene, Oregon

I have worked on a variety of projects, including large projects which included a team of software and hardware people, as well as some individual projects in which I was responsible for the development and delivery of a software product. My responsibilities have included the design, implementation, and testing of mathematical and communications algorithms for use in systems which utilize and control external devices such as bar code scanners, scanner/scale combinations, and robot arms. Several of these projects have been real-time, interrupt-driven systems. All of them have utilized peripheral devices. Communications with the scanners utilizes a variety of interfaces including RS-232, RS-485, and Optically Coupled. Two of the main projects on which I was the main software person, involved designing , coding and debugging programs to implement communications between a bar code scanner and a PC computer. These programs utilized the revectoring of interrupt handlers and were interrupt driven. The communications were performed by *using interrupts generated by an RS-485 board on a selectable IRQ line.* I have taught three C language classes on site to a total of approximately 50 people. In addition, I have acted as a resource in providing programming assistance to other people on an as needed basis.

Languages : C, Pascal

March 1991 to present

Instructor, Continuation Center, University of Oregon

I completed the training for and am certified as an instructor in the Apple Developer University program. I have taught the User Centered Design and Macintosh Programming Fundamentals classes. These are classes which are oriented towards people with an interest in writing software for the Macintosh. The MPF course covered the basics of Macintosh programming using Think C. The UCD course covered the basics of the Macintosh user interface. In addition, I have taught several introductory mathematics classes at the UofO Eugene campus. Most recently, I taught an introductory C programming class to a group of visiting German students. I have developed and presented two seminars on Object Oriented Design and the C++ language. These classes are oriented towards experienced programmers.

Languages : Think C

September 1985 to June 1989 and March 1991 to June 1991

Instructor, Computer and Information Sciences Department, University of Oregon

I taught a variety of computer science classes, including Data Structures, Computer Organization, Advanced Numerical Processing using Fortran, and Introduction to Computing. Class size ranged from twenty to almost two hundred. **Languages : Fortran, C, Pascal**

March 1989 to June 1990

Instructor, Data Processing Department, Lane Community College

I have taught several programming and introductory computer classes. One C programming class was taught on site at Spectra Physics. All of the others have been taught on the Lane Community College main campus. Typical class size has been from twenty to thirty students.

Languages : C and Pascal

September 1984 to June 1992

Instructor, Mathematics Department, University of Oregon

My responsibilities included teaching two or three classes per term. The classes included algebra, trigonometry, calculus, and discrete mathematics. Class size ranged from twenty to well over one hundred. I was also the supervisor of the Trigonometry and Algebra sections on several occasion. I served on the textbook selection committees for Trigonometry and Algebra.

References :
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Born 8-15-51
Married, with three children
Excellent health

Interests
Family, softball, racquetball, bicycling, reading, hiking.

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GRADUATE AND UNDERGRADUATE SCHOOLS ATTENDED:
University of Oregon
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DEGREES AWARDED:
Master of Arts, 1992, University of Oregon
Diplom-Vorprüfung, 1988, RWTH Aachen

AREAS OF SPECIAL INTEREST:
Computational Neuroscience
Neuroethology

PROFESSIONAL EXPERIENCE:

Graduate Teaching Fellow, Department of Biology, University of
Oregon, Eugene, 1990

Tutor, Department of Mathematics, RWTH Aachen, Aachen, 1988-89

Computer Operator (during military service), LTKdo Münster, Münster, 1986

Teacher, Computer Science, VHS Emsdetten, Emsdetten, 1984-85

AWARDS AND HONORS:
McDonnell and Pew Foundation Fellowship, 1991
MBL Stipend for course "Methods in Computational Neuroscience",
Woods Hole, 1990
Fulbright Stipend, 1989-91
Studienstiftung des Deutschen Volkes stipend, 1987-88

PUBLICATIONS:
Kautz D, Wagner H, Takahashi TT (1992) A computer model for acoustic motion-
direction sensitivity in the barn owl. In: Rhythmogenesis in neurons and
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N, Richter DW, eds), p 727. New York: Thieme.

CLIFFORD H KELLER

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RESEARCH INTERESTS

Neuronal processing of complex sensory stimuli and transformations from sensory coding to motor control. Evolution and function of the acousticolateralis system. Behavioral ecology of weakly electric fishes.

PERSONAL

born: June 9, 1952
married: Sally Brumley Keller
two children: Kinsey (b. 1981), Adrienne (b. 1984)

EDUCATION

BA   1977 Zoology, University of Washington, Seattle

MSc 1981 Ecology and Behavioral Biology, University of Minnesota, Minneapolis

PhD 1989 Oceanography, Scripps Institution of Oceanography
          University of California, San Diego
          "A Sensory-Motor Interface in Weakly Electric Fishes"

RELATED EXPERIENCE

Postdoctoral Research with Dr. Terry Takahashi (Acoustic Motion Detection in Barn Owls; Sept. '89 to present)

Additional Courses:
* Neural Systems and Behavior, Marine Biological Laboratories, 1984
* Advanced Invertebrate Zoology (Crustacea), Friday Harbor Laboratories, 1980

Field Collecting and Research:
* Research expedition to Pakitza, Peru ('90) to study biodiversity of electric fish in the upper Amazonian rain forest
* Three expeditions to Venezuela ('87, '88, '89) to collect electric fish for blood analysis and for transport to San Diego for laboratory studies
* Collection of electric fish in the Darien, Panama ('85)
* Research cruise to Galapagos Hydrothermal Vents (DSRV Alvin; '85)
* Several short cruises to support oceanographic research

Research Assistantships:
* with Dr. Walter Heiligenberg (Information Processing in Weakly Electric   Fishes; '84 to '89)
* with Dr. Robert Hessler (Ecology of Hydrothermal Vent Fauna, '83 to '84)
* with Dr. Robert Hessler (Deep-Sea Megafaunal Abundance, '82 to '83)

Teaching Assistantships:
* Introductory Biology (2X), Introductory Zoology (3X), Invertebrate Zoology, Minnesota Freshwater Invertebrates

AWARDS AND GRANTS

* NRSA (NIH): "Neuroethology of Acoustic Motion Perception;" '91-94
* Smithsonian Institution BIOLAT program, "Diversity of Gymnotiform Fish   in Western Amazonas (Peru);" '90 and '92
* Research Assistant, Scripps Institution of Oceanography, '81 - '89
* Office of Graduate Studies and Research, Small Grants Program
* University of California Regents Fellowship, '81

PROFESSIONAL SOCIETIES

* AAAS
* American Society of Zoologists
* International Society for Neuroethology
* JB Johnston Club
* Society for Neuroscience

HONORS

* Donald B Lindsley Award for Behavioral Neuroscience (1990), presented annually by the Society for Neuroscience
* Honorable mention, Capranica Foundation Award in Neuroethology (1990)

INVITED PRESENTATIONS

"Transformations from sensory processing to motor control in the diencephalon of weakly electric fishes"; 2nd International Congress of Neuroethology, Berlin Sept. 1989

PUBLICATIONS

Takahashi TT, Keller CH (in press) Simulated motion enhances neuronal selectivity for a sound localization cue in background noise. *J Neurosci*

Takahashi TT, Keller CH (1992) Commissural connections mediate inhibition for the computation of interaural level difference in the barn owl. *J Comp Physiol A* 170:161-169

Keller CH, Kawasaki M, Heiligenberg W (1991) The control of pacemaker modulations for social communication in the weakly electric fish Sternopygus. J Comp Physiol A 169:441-450

Heiligenberg W, Keller CH, Metzner W, Kawasaki M (1991) Structure and function of neurons in the complex of the nucleus electrosensorius of the gymnotiform fish Eigenmannia: Detection and processing of electric signals in social communication. J Comp Physiol A 169:151-164

Keller CH, Maler L, Heiligenberg W (1990) Structural and functional organization of a sensory-motor interface in the weakly electric fish, Eigenmannia. J Comp Neurol 293:347-376

Devor M, Keller CH, Ellisman MH (1990) Spontaneous discharge of afferents in a neuroma reflects original receptor tuning. Brain Research 517(1-2):245-250

Dye J, Heiligenberg W, Keller CH, Kawasaki M (1989) Different classes of glutamate receptors mediate distinct behaviors in a single brainstem nucleus. PNAS 86:8993-8997

Devor M, Keller CH, Deerinck TJ, Levinson SR, Ellisman MH (1989) Na^+-Channel accumulation on axolemma of afferent endings in nerve-end neuromas in Apteronotus. Neurosci Letters 102:149-154

Keller CH, Heiligenberg W (1989) From distributed sensory processing to discrete motor representations in the diencephalon of the electric fish, Eigenmannia. J Comp Physiol A 164:565-576

Hessler RR, Smithey WM, Boudrias MA, Keller CH, Lutz RA, Childress JJ (1988) Temporal change in megafauna at the Rose Garden hydrothermal vent. Deep Sea Res 35:1681-1709

Keller CH (1988) Stimulus discrimination in the diencephalon of Eigenmannia: the emergence and sharpening of a sensory filter. J Comp Physiol A 162:747-757

Meyer JH, Leong M, Keller CH (1987) Hormone-induced and maturational changes in electric organ discharges and electroreceptor tuning in the weakly electric fish Apteronotus. J Comp Physiol A 160:385-394

Rose G, Keller CH, Heiligenberg W (1987) 'Ancestral' neural mechanisms of electrolocation suggest a substrate for the evolution of the jamming avoidance response. J Comp Physiol A 160:491-500

Keller CH, Zakon HH, Sanchez DY (1986) Evidence for a direct effect of androgens upon electroreceptor tuning. J Comp Physiol A 158:301-310

PUBLICATIONS (cont.)

Keller CH (1985) Benthic megafauna at deep-sea study areas W-N and E-N. Sandia National Laboratories Annual Report.

Hessler RR, Smithey WM Jr., Keller CH (1985) Spatial and temporal variation of giant clams, tube worms and mussels at deep-sea hydrothermal vents. Biol Soc Wash Bull 6:411-428

ABSTRACTS

Takahashi TT, Keller CH (1992) Unmasking of auditory targets and enhancement of selectivity to a sound localization cue by simulated motion in the owl's inferior colliculus. Soc Neurosci Abstr 18:

Keller CH, Kawasaki M, Heiligenberg W, Kennedy G, Metzner W (1991) A sublemniscal prepacemaker nucleus in gymnotiform electric fish depolarizes relay cells of the pacemaker nucleus via NMDA-type receptors. Soc Neurosci Abstr 17:1406

Keller CH, Kawasaki M, Heiligenberg W (1989) Intracellular labelling of physiologically defined cells within a diencephalic sensory-motor interface of weakly electric knifefish. Soc Neurosci Abstr 15:1136

Kawasaki M, Keller CH, Heiligenberg W (1989) Modulations of the electric-organ pacemaker nucleus of gymnotiform electric fish by pharmacologically distinguishable pathways. Soc Neurosci Abstr 15:1135

Keller CH, Maler L, Heiligenberg W (1989) The anatomical and functional organization of a sensory-motor interface, the nucleus electrosensorius of Eigenmannia. 2nd International Congress of Neuroethology

Keller CH, Kawasaki M, Heiligenberg W (1988) Pacemaker modulations in the electric fish Sternopygus. Soc Neurosci Abstr 14:204

Devor M, Keller CH, Deerink T, Levinson SR, Ellisman M (1988) Sodium channels accumulate on axolemma of hyperexciteable neuroma afferents. Soc Neurosci Abstr 14:1128

Dye J, Heiligenberg W, Keller CH, Kawasaki M (1988) Behaviorally distinct pacemaker modulations mediated by differing glutamate receptors in electric fish. Soc Neurosci Abstr 14:204

Keller CH, Heiligenberg W (1987) A few cells within Eigenmannia's diencephalic electrosensorius complex would be sufficient to discriminate the sign of the difference frequency in the jamming avoidance response. Soc Neurosci Abstr 13:623

Rose G, Keller CH, Heiligenberg W (1986) Sternopygus offers insight into the functional role of 'sign selective' neurons in the torus semicircularis. Soc Neurosci Abstr 12:200

MANUSCRIPTS IN PREPARATION:

Hagedorn M, Keller CH The diversity of gymnotiform fishes near Pakitza, Peru

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Current Position:

Assistant Professor of Biology, Institute of Neuroscience,
University of Oregon

Education and Experience:

1982-1988   Research Fellow, Division of Biology, California
             Institute of Technology.
Research topic: Neural mechanisms of sound localization.
Supervisor: Professor Mark Konishi.

Ph.D. 1981   State University of New York, Health Science Center at
              Brooklyn.
Thesis topic: Experimental neuroanatomy of the visual system.
Thesis title: The Organization of the Lateral Thalamus of the
              Hooded Rat.
Thesis advisor: Professor Frank Scalia

M.S. 1977 California State University, Long Beach
Thesis topic: Neuroplasticity in the visual system.
Thesis title: Sprouting in the Retinofugal Pathways of the Rat.
Thesis advisor: Professor Kenneth M. Gregory

B.S. 1975   University of California, Irvine
Major: Biological Science

Research Interest: Sensory processing and the neural basis of perception.

Honors and Awards:

1989-Present   National Institutes of Health FIRST Award
       "Generation of Auditory Spatial Receptive Fields"
1989-Present   Office of Naval Research Grant "Detection of
       Acoustic Motion by Passive Listening"
1982   National Institutes of Health Postdoctoral Fellowship
1981   Del E. Webb Fellowship, California Institute of Technology
1977-1981 Competitive Graduate Teaching Assistantship, State
       University of New York
1975 Graduation with Honors in Biology University of California,
       Irvine

Affiliations:

Society for Neuroscience
American Association of Anatomists
International Society for Neuroethology

Citizenship: United States

Publications:

Takahashi, T.T. and C.H. Keller Simulated motion enhances neuronal selectivity for a sound localization cue in background noise. *in press* J. Neurosci.

Takahashi, T.T. and C.H. Keller 1992 Commissural connections mediate inhibition for the computation of interaural level difference in the owl. J. Comp. Physiol. A. 170:161-169.

Wagner, H. and T.T. Takahashi 1990 Neurons in the midbrain of the barn owl are sensitive to the direction of apparent acoustic motion. Naturwissenchaften 77:439-442.

Takahashi, T.T. 1989 The neural coding of auditory space. J. Exp. Biol. 146:307-322.

Takahashi, T. T. 1989 The construction of an auditory space-map. Ann. NY Acad. Sci. 563 (*Modulation of Defined Vertebrate Neural Circuits*) 101-113.

Takahashi, T.T., H. Wagner, and M. Konishi, 1989. The role of commissural projections in the representation of bilateral auditory space in the barn owl's inferior colliculus. J. Comp. Neur. 281:545-554

Takahashi, T.T. and M. Konishi, 1988 The projections of the cochlear nuclei and nucleus laminaris to the inferior colliculus of the barn owl. J. Comp. Neur. 274:190-211.

Takahashi, T.T. and M. Konishi, 1988 The projections of nucleus angularis and nucleus laminaris to the lateral lemniscal nuclear complex of the barn owl. J. Comp. Neur. 274:212-238.

Konishi, M., T.T. Takahashi, H. Wagner, W.E. Sullivan, and C.E. Carr, 1988 Neurophysiological and Anatomical Substrates of Sound Localization in the Owl. In *Auditory Function* G.M. Edelman, W.E. Gall, and W.M. Cowan (eds.) John Wiley and Sons, New York, Chichester, Brisbane, Toronto, Singapore. pp 721-745.

Wagner, H., T.T. Takahashi, and M. Konishi, 1987 Representation of interaural time difference in the central nucleus of the barn owl's inferior colliculus. J. Neurosci., 7:3105-3116.

Takahashi, T.T., C.E. Carr, N. Brecha, and M. Konishi, 1987 Calcium binding protein-like immunoreactivity labels the terminal field of nucleus laminaris of the barn owl. J. Neurosci., 7:1843-1856.

Takahashi, T. and M. Konishi, 1986 Selectivity for interaural time difference in the owl's midbrain. J. Neurosci., 6:3413-3422.

Takahashi, T., 1985 The organization of the lateral thalamus of the hooded
    rat. J. Comp. Neur., 231:281-309. [Incorporated into: *The Rat Brain in
    Stereotaxic Coordinates, 2nd Ed.* by G. Paxinos and C. Watson. Academic
    Press, 1986]

Takahashi, T., A. Moiseff, and M. Konishi, 1984 Time and intensity cues are
    independently processed in the barn owl's auditory system. J.
    Neurosci., 4:1781-1786.

Konishi, M., W.E. Sullivan, and T. Takahashi, 1984 The owl's cochlear nuclei
    process different sound localization cues. J. Acoust. Soc. Amer.
    78:360-364.

Giolli, R.A., L.C. Towns, T. Takahashi, A.N. Karamanlidis, and D.D. Williams,
    1978 An autoradiographic study of visual cortical Area 1 to the
    thalamus, pretectum and superior colliculus in the rabbit. J. Comp.
    Neur. 180:743-752.

Colloquia:

January 1982 Seminar speaker: Department of Anatomy, University of
California, Irvine. "The organization of the lateral thalamus of the hooded
rat".

October 1986 Seminar speaker: Center for Hearing Sciences, Johns Hopkins
University. "Sound localization in the barn owl".

March 1987 Seminar speaker: Department of Psychology, Brown University.
"The neural mechanisms of sound localization in the barn owl".

April 1987 Seminar speaker: Section of Neurobiology and Behavior, Cornell
University. "The neuroethology of sound localization in the barn owl".

April 1987 Seminar speaker: Institute of Neuroscience, University of Oregon.
"The neural mechanisms of sound localization in the barn owl".

September 1988 Participant and speaker: National Institutes of Mental Health
Conference on the Modulation of Defined Vertebrate Neural Circuits. "The
construction of an auditory space-map".

October 1988 Seminar speaker: Department of Biology, Portland State
University. "Time, Space, and the Owl: Neural Representation of Space."

December 1988 Seminar speaker: Robert Dow Neurological Sciences Institute
and Good Samaritan Hospital, Portland, Oregon. "Sound Localization in the
Barn Owl: Building Maps and Cracking Neural Codes."

April 1989 Participant and speaker: Conference on Sensory Coding and
Processing (sponsored: Journal of Experimental Biology) Portpatrick,
Scotland. "The Neural Coding of Auditory Space."

August 1989 Seminar speaker: Department of Zoology. Technical University of